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A TEXT BOOK

OF

PHYSIOLOGY

A TEXT BOOK

OF

PHYSIOLOGY

BY

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WITH ILLUSTRATIONS.

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SINCE the time when I was engaged in preparing the last edition of this Part of my Text Book, the progress of our knowledge in the branch of Physiology dealt with in it has been very great, has indeed been remarkable. It has compelled me wholly to rewrite numerous paragraphs; I have thought it wiser to use a free hand in this respect rather than to attempt merely to correct or add to what I had written before.

My friend, Prof. Sherrington, has given me throughout such large help, that I have thought it due to him that his name should appear with mine on the title-page; but I have also received great assistance from other friends, more especially Dr Langley and Dr H. Anderson.

M. FOSTER.

CAMBRIDGE,
August, 1897.

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BOOK III.

THE CENTRAL NERVOUS SYSTEM AND ITS INSTRUMENTS.

CHAPTER I.

THE SPINAL CORD.

SEC. 1. ON SOME FEATURES OF THE SPINAL NERVES.

§ 558. WE have called the muscular and nervous tissues the master tissues of the body; but a special part of the nervous system, that which we know as the central nervous system, the brain and spinal cord, is supreme among the nervous tissues and is master of the skeletal muscles as well as of the rest of the body. We have already (Book I. Chap. III.) touched on some of the general features of the nervous system, and have now to study in detail the working of the brain and spinal cord. We have to inquire what we know concerning the laws which regulate the discharge of efferent impulses from the brain or from the cord, and to learn how that discharge is determined on the one hand by intrinsic changes originating, apparently, in the substance of the brain or of the cord, and on the other hand by the nature and amount of the afferent impulses which reach them along afferent nerves.

As we shall see the study of the spinal cord cannot be wholly separated from that of the brain, the two being very closely related. Nevertheless it will be of advantage to deal with the spinal cord by itself so far as we can. The spinal bulb (medulla oblongata) we shall consider as part of the brain. But before we speak of the spinal cord itself, it will be desirable to say a few words concerning the spinal nerves, that is to say the nerves which issue from the spinal cord.

We have already seen (§ 96) that each of the spinal nerves arises by two roots, an anterior root attached to the ventral or anterior surface, and a posterior root attached to the dorsal or posterior surface of the cord. We have further seen that the latter bears a ganglion, a 'ganglion of the posterior root' or 'spinal ganglion,' and we have (§ 97) studied the structure of this ganglion.

We stated at the same time that while the trunk of a spinal nerve contained both efferent and afferent fibres, the efferent fibres were gathered up into the anterior root and the afferent fibres into the posterior root; but we gave no proof of this statement.

§ **559**. Before we proceed to do so, it will be as well to say a few words on the terms 'efferent' and 'afferent.' By efferent nerve fibres we mean nerve fibres which in the body usually carry impulses from the central nervous system to peripheral organs. Most efferent nerve fibres carry impulses to muscles, striated or plain, and the impulses passing along them give rise to movements; hence they are frequently spoken of as 'motor' fibres. But all efferent fibres do not end in or carry impulses to muscular fibres; we have seen for instance that some efferent fibres are secretory. Moreover all the nerve fibres going to muscular fibres do not serve to produce movement; some of them, as in the case of certain vagus fibres going to the heart, are inhibitory and may serve to stop movement.

By 'afferent' nerve fibres we mean nerve fibres which in the body usually carry impulses from peripheral organs to the central nervous system. A very common effect of the arrival at the central nervous system of impulses passing centripetally along afferent fibres is that change in consciousness which we call a 'sensation'; hence afferent fibres are often called 'sensory' fibres, and the nervous impulses passing centripetally along them, sensory impulses. But as we have already in part seen, and as we shall shortly see in greater detail, the central nervous system may be affected by centripetal impulses, and that in several ways, quite apart from the development of any such change of consciousness as may be fairly called a sensation. We shall see reason for thinking that centripetal impulses reaching the spinal cord, and indeed other parts of the central nervous system, may modify reflex or automatic or other activity without necessarily giving rise to a "sensation." Hence it is advisable to reserve the terms 'efferent' and 'afferent' as more general modes of expression than 'motor' or 'sensory.'

We have seen in treating of muscle and nerve, that the changes produced in the muscle serve as our best guide for determining the changes taking place in a motor nerve; when a motor nerve is separated from its muscle (§ 72) the only change which we can appreciate in it is an electrical change. Similarly in the case of an afferent nerve, the central system is our chief teacher; in a bundle of afferent fibres isolated from the central nervous system, in a posterior root of a spinal nerve for instance, the only change which we can appreciate is an electrical change. To learn the characters of afferent impulses we must employ the central nervous system. But in this we meet with difficulties. In studying the phenomena of motor nerves we are greatly assisted by two facts. First, the muscular contraction by which we judge of what is going on in the nerve is a comparatively simple thing; one contraction differs from another by such features only as extent or amount, duration, frequency of repetition and the like, and all such differences are capable of exact measurement. Secondly, when we apply an artificial stimulus, such as an electric shock, directly to the nerve itself, the effects, so far as we at present know, differ in degree only from those which result when the nerve is set in action by a natural stimulus, such as the will. When we come, on the other hand, to investigate the phenomena of afferent nerves, our labours are for the time rendered heavier, but in the end more fruitful, by the following circumstances:—First, when we judge of what is going on in an afferent nerve by the effects which stimulation of the nerve produces in some central nervous organ, in the way of exciting or modifying reflex action, or modifying automatic action, or affecting consciousness, we are met on the very threshold of every enquiry by the difficulty of clearly distinguishing the events which belong exclusively to the afferent nerve from those which belong to the central organ. Secondly, the effects of applying a stimulus to the peripheral end-organ of an afferent nerve are very different from those of applying the same stimulus directly to the nerve-trunk; this may be shewn by the simple experience of comparing the sensation caused by bringing any sharp body into contact with a nerve laid bare in a wound with that caused by contact of an intact skin with the same body. These and like differences reveal to us a complexity of impulses, of which the phenomena of motor nerves gave us hardly a hint.

We shall further see in detail later on that our consciousness may be affected in many different ways by afferent impulses; we must distinguish not only sensory from other afferent impulses, but also different kinds of sensory impulses from each other. Certain afferent nerves are spoken of as nerves of special sense, and the nature of the afferent impulses passing along these special nerves together with the modifications of consciousness caused by arrival of these impulses at the central nervous system constitute by themselves a complex and difficult branch of study. In some of the problems connected with the central nervous system we shall have to appeal to the results of a study of these special senses; but, on the other hand, a knowledge of the central nervous system is necessary to a proper understanding of the special senses; and on the whole it will be more convenient to study the former before the latter.

We may, however, digress here to remark that the question whether an afferent impulse differs in itself from an efferent impulse is one of great difficulty. It is true that the electrical changes, which alone as we have said we can appreciate in an isolated piece of nerve, appear to be the same in both kinds of fibres; in each the electrical change is propagated in both directions and possesses the same features. But it would be hazardous to insist too much on this. Moreover, we must remember that what we call a nervous impulse, especially one provoked by artificial stimulation, constitutes a gross change in the nerve fibre, and that changes of a finer, more delicate nature, such as cannot be shewn by the coarse methods used to detect a 'nervous impulse,' may take place in, and be propagated along, a nerve fibre. We shall have occasion immediately to point out that the condition of an afferent nerve fibre along its whole length is dependent on a nerve cell in the ganglion of the posterior root; the fibre when cut off from the nerve cell degenerates and dies. This means that in the intact fibre certain influences are propagated along the fibre from the cell in the ganglion to the peripheral endings of the fibre, that is to say in a direction the opposite of that taken by the ordinary centripetal nervous impulses; and it may be that in like manner in efferent fibres some influences are propagated centripetally from the peripheral endings to the central nervous system. Our knowledge of these influences is extremely limited; but it is important to bear in mind the possibility of their occurrence. And we had this in view, when above, in speaking of efferent and afferent fibres, we used the phrase "usually carry impulses."

§ 560. The proof that the afferent and efferent fibres which are both present in the trunk of a spinal nerve are parted at the roots, the efferent fibres running exclusively in the ventral or anterior root and the afferent fibres exclusively in the dorsal or posterior root, is as follows.

When the anterior root is divided, the muscles supplied by the nerve cease to be thrown into contractions either by the will, or by reflex action, while the structures to which the nerve is distributed retain their sensibility. During the section of the root, or when the proximal stump, that connected with the spinal cord, is stimulated, no sensory effects are produced. When the distal stump is stimulated, the muscles supplied by the nerve are thrown into contractions. When the posterior root is divided, the muscles supplied by the nerve continue to be thrown into action by an exercise of the will or as part of a reflex action, but the structures to which the nerve is distributed lose the sensibility which they previously possessed. During the section of the root, and when the proximal stump is stimulated, sensory effects are produced. When the distal stump is stimulated no movements are called forth. These facts demonstrate that sensory impulses pass exclusively by the posterior root from the peripheral to the central organs, and that motor impulses pass exclusively by the anterior root from the central to the peripheral organs; and so far as our knowledge goes the same holds good not only for sensory and motor but also for all centripetal and centrifugal impulses.

An exception must be made to the above general statement, on account of the so-called "recurrent sensibility" which is witnessed in conscious mammals, under certain circumstances. It sometimes happens that when the distal stump of the divided anterior root is stimulated, signs of pain are witnessed. These are not caused by the concurrent muscular contractions or cramp which the stimulation occasions, for they persist after the whole trunk of the nerve has been divided some little way below the union of the roots above the origins of the muscular branches, so that no contractions take place. They disappear when the posterior root is subsequently divided, and they are not seen if the mixed nerve trunk be divided close to the union of the roots. The phenomena are probably due to the fact, that bundles of sensory fibres of the posterior root after running a short distance down the mixed trunk turn back and run upwards in the anterior root, (being distributed probably to the pia mater) and by this recurrent course give rise to the recurrent sensibility.

Further, certain experimental and histological results have been brought forward to shew that the posterior roots do or may contain efferent fibres carrying impulses to the plain muscular fibres such as those of the intestines and blood vessels; but the evidence for this is not at present sufficiently conclusive to render invalid the same general statement.

§ 561. Concerning the *ganglion* on the posterior root, we may say definitely that we have no evidence that it can act as a centre of reflex action; nor have we any evidence that it can spontaneously give origin to efferent impulses and thus act as an automatic centre, as can the central nervous system itself. The bodies of the nerve-cells behave somewhat differently from the axis-cylinders at some distance from the cells, though, as we have seen, these are in reality processes of the nerve cells; thus the nerve cells in the ganglion are more sensitive to certain poisons (ex. gr. nicotin) than are the nerve fibres of the nerve trunk. But beyond this, our knowledge concerning the function of the ganglion is almost limited to the fact that it is in some way intimately connected with the nutrition of the nerve. As we have already (§ 83) said, when a mixed nerve trunk is divided the peripheral portion degenerates from the point of section downwards towards the periphery. The central portion does not so degenerate, and if the length of nerve removed be not too great, the central portion may grow downwards along the course of the degenerating peripheral portion, and thus regenerate the nerve. This degeneration is observed when the mixed trunk is divided in any part of its course from the periphery to close up to the ganglion. When the posterior root is divided between the ganglion and the spinal cord, the portion attached to the spinal cord degenerates, but that attached to the ganglion remains intact. When the anterior root is divided, the proximal portion in connection with the spinal cord remains intact, but the distal portion between the section and the junction with the other root degenerates; and in the mixed nerve-trunk many degenerated fibres are seen, which, if they be carefully traced out, are found to be motor (efferent) fibres. If the posterior root be divided carefully between the ganglion and the junction with the anterior root, the small portion of the posterior root left attached to the peripheral side of the ganglion above the section remains intact, as does also the rest of the root from the ganglion to the spinal cord, but in the mixed nerve-trunk are seen numerous degenerated fibres, which when examined are found to have the distribution of sensory (afferent) fibres. Lastly, if the posterior ganglion be excised, the whole posterior root degenerates, as do also the sensory (afferent) fibres of the mixed nerve trunk. Putting all these facts together, it would seem that the nutrition or growth of the efferent and afferent fibres takes place in opposite directions, and starts from different nutritive or 'trophic' centres. The afferent fibres grow away from the ganglion either towards the periphery, or towards the spinal cord. The efferent fibres grow outwards from the spinal cord towards the periphery. The afferent fibre is essentially a process of a cell in the ganglion: the axis-cylinder of the fibre running in the root and that of the fibre running along the nerve-trunk, are divisions of the elongated process of a nerve cell. The axis-cylinder of the efferent fibre on the other hand is a process of a nerve cell in the spinal cord. In both cases the axis-cylinder degenerates and dies when it is separated from the part of the cell surrounding the nucleus; and the degeneration of the axis-cylinder entails the degeneration of its wrappings, the medulla, and so of the whole nerve. When an amoeba or other unicellular organism is so divided that one moiety retains the nucleus and the other is simply a portion of cell-body without a nucleus, it is observed that while the latter moiety speedily dies, the former moiety continues to live and may regenerate the whole body. Similarly the nerve fibre cut away from its nucleus dies, but the part retaining the nucleus continues to live and may regenerate the whole fibre. Hence though efferent and afferent fibres degenerate in different directions the cause of the degeneration is the same in the two cases.

This difference in their mode of nutrition is frequently of great help in investigating the relative distribution of efferent and afferent fibres. When a posterior root is cut beyond the ganglion, or the ganglion excised, all the afferent nerves degenerate, and in the mixed nerve branches these afferent fibres, by their altered condition, can readily be traced. Conversely, when the anterior roots are cut, the efferent fibres alone degenerate, and can be similarly recognized in a mixed nerve tract. When the anterior root is divided some few fibres in it do not, like the rest, degenerate, and when the posterior root is divided, a few fibres in the anterior root are seen to degenerate like those of the posterior root; these appear to be the fibres which give to the anterior root its "recurrent sensibility." In the case of certain spinal nerves at all events, it has also been ascertained that when the posterior root is divided, while most of the fibres in the part of the root thus cut off from the ganglion but left attached to the cord degenerate, some few do not. These few appear to have their trophic centre not in the ganglion, but in some part of the spinal cord itself; we shall refer to these later on.

This method of distinguishing nerve fibres by the features of their degeneration, called the "degeneration method," or sometimes from the name of the physiologist who introduced it, the "Wallerian method," has proved of great utility. Thus in the vagus nerve which is composed not only of fibres which spring from the real vagus root but also of fibres proceeding from the spinal accessory roots, the two may be distinguished by section of the vagus and spinal accessory roots respectively. We shall presently see that this method may be applied to the differentiation of tracts of fibres in the brain and spinal cord.

SEC. 2. THE STRUCTURE OF THE SPINAL CORD.

§ **562**. Lying within the vertebral canal the spinal cord is protected by its 'membranes,' the dura mater, the arachnoid membrane and the pia mater. The consideration of the arrangement of these membranes and of the structure of the dura mater and arachnoid we will leave until we come to speak of the vascular and lymphatic supplies of the central nervous system; the histology of the pia mater may more fitly come with that of the spinal cord itself.

Along its whole length from its junction with the bulb to its termination in the *filum terminale* the spinal cord, while possessing certain general features, is continually changing as to special features. It will be convenient to study first the general structure of some particular part, for instance the middle of the thoracic (dorsal)[1] region, and afterwards to point out the special features which obtain in the several regions.

A transverse vertical section of either a fresh or a hardened and prepared spinal cord at the thoracic region possesses an outline which is roughly speaking circular. In the middle of the anterior or ventral surface is a vertical fissure, *the ventral* or *anterior fissure* (Fig. 96, *A. F.*) running some way across the thickness of the cord from the ventral towards the dorsal surface. Opposite to it on the posterior or dorsal surface is a corresponding deeper but narrower, *dorsal* or *posterior fissure* (Fig. 96, *P. F.*) which, however, as we shall see, differs materially in nature from the

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[1] It is very desirable to use the terms 'dorsal' and 'ventral' for the parts of the cerebro-spinal axis which lie respectively near the dorsal or back part, and the ventral or belly part of the body, instead of the terms posterior and anterior; but if this is done, the use of the word dorsal to denote the region of the cord between the lumbar and cervical regions is apt to lead to confusion; hence the introduction of the word thoracic. If this use of dorsal and ventral be adhered to, before and behind, above and below, may conveniently be used to denote nearer the head and nearer the tail (or coccyx) respectively; anterior and posterior may also be used in the same sense.

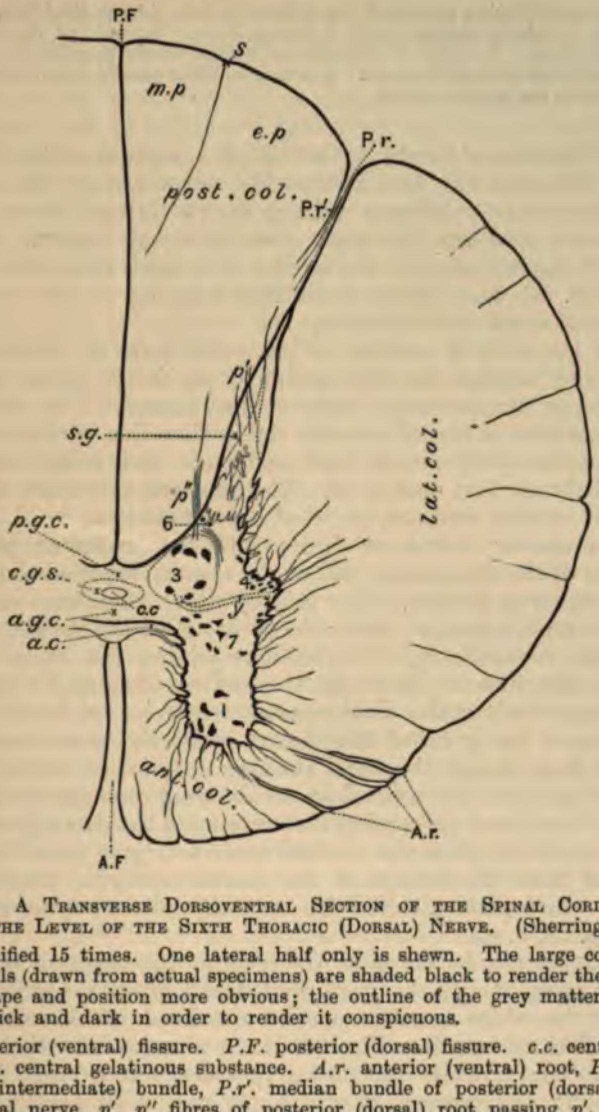

FIG. 96. A TRANSVERSE DORSOVENTRAL SECTION OF THE SPINAL CORD (HUMAN) AT THE LEVEL OF THE SIXTH THORACIC (DORSAL) NERVE. (Sherrington.)

Magnified 15 times. One lateral half only is shewn. The large conspicuous nerve-cells (drawn from actual specimens) are shaded black to render their relative size, shape and position more obvious; the outline of the grey matter has been made thick and dark in order to render it conspicuous.

A.F. anterior (ventral) fissure. *P.F.* posterior (dorsal) fissure. *c.c.* central canal. *c.g.s.* central gelatinous substance. *A.r.* anterior (ventral) root, *P.r.* lateral (or intermediate) bundle, *P.r'.* median bundle of posterior (dorsal) root of spinal nerve, *p'*, *p''* fibres of posterior (dorsal) root passing *p'*, indirectly through the substance of Rolando, *p''*, directly into grey matter. *a.g.c.* anterior (ventral) grey commissure. *p.g.c.* posterior (dorsal) grey commissure. *a.c.* anterior (ventral) white commissure. *ant. col.* anterior (ventral) column. *lat. col.* lateral column. *post. col.* posterior (dorsal) column. *s.g.* the substance of Rolando. *s.* septum marking out the external posterior (dorsal) column or column of Burdach, *e.p.*, from the median posterior (dorsal) column or column of Goll, *m.p.*

1. cells of the anterior (ventral) horn. 2. marks position of a group of small cells of considerable constancy and extent in the mammalian cord, the "middle cells." 3. posterior (dorsal) vesicular column or vesicular cylinder,

or column of Clarke; the area of the cylinder is defined by a dotted line. 4. cells of the intermedio-lateral tract or lateral horn. 6. cells of the posterior (dorsal) horn. 7. cells of the anterior ventral cervix peculiar to this and adjoining segments of the cord. *y*. a tract of fibres passing from the vesicular cylinder to the lateral column.

anterior fissure, and ought to be called a septum rather than a fissure. Between the two fissures the substance of the cord is reduced to a narrow isthmus uniting the two lateral halves, which in a normal cord are like each other in every respect. In the middle of the isthmus lies the section of a small canal, *the central canal* (Fig. 96, *c.c.*), which is all that remains of the relatively wide neural canal of the embryo.

Each lateral half consists of an outer zone of *white matter* surrounding, except at the isthmus, an inner more or less crescentic, or comma shaped mass of *grey matter*. The convexity of each crescent is turned towards the median line of the cord, the two crescents being placed back and back and joined together by the isthmus just spoken of. The somewhat broader anterior extremity of the crescent, or head of the comma, is called the *ventral* (*anterior*) *cornu* or *horn*; and the narrower posterior extremity of the crescent, or tail of the comma, is called the *dorsal* (*posterior*) *cornu* or *horn*. The part by which each horn is joined on to the middle part of the crescent is called the *cervix*, ventral and dorsal respectively. The isthmus joining the backs of the two crescents, like the crescents themselves, consists, for the most part, of grey matter, the band running posterior or dorsal to the central canal being called the *dorsal* (*posterior*) *grey commissure* (Fig. 96, *p. g. c.*), and the band running anterior or ventral to the canal being called the *ventral* (*anterior*) *grey commissure* (Fig 96, *a. g. c.*). The dorsal (posterior) fissure touches the dorsal (posterior) grey commissure, but the ventral (anterior) grey commissure is separated from the bottom of the ventral (anterior) fissure by a band of white matter, called the *ventral* (*anterior*) *white commissure* (Fig. 96, *a. c.*).

If the section be taken at the level of the origin of a pair of spinal nerves, it will be seen that the ventral (anterior) root, piercing the white matter opposite the head of the comma in several distinct bundles (Fig. 96, *A.r.*), plunges into the ventral (anterior) cornu, while the dorsal (posterior) root (Fig. 96, *P.r.*, *P.r.*), having the appearance of a single undivided bundle, passes, in part at least, into the dorsal (posterior) horn. Both roots are dispersed lengthways along the cord, the hinder roots of one nerve being close to the foremost roots of the nerve below, but it is only the ventral (anterior) roots which are dispersed sideways. The compact bundle of the dorsal (posterior) root divides, with tolerable sharpness, the white matter in each lateral half of the cord into a dorsal (posterior) portion lying between the dorsal (posterior) fissure and the dorsal (posterior) root (Fig. 96, *post. col.*), which portion since, as we shall see, it runs in the form of a column along the length of the cord, is called the *posterior column*, and into a portion lying to the outside of the dorsal (posterior) root between it and the ventral (anterior) fissure, called the *antero-lateral column.* This latter may be considered as further divided, by the entrance of the ventral (anterior) roots into a *lateral column* (Fig. 96, *lat. col.*) between the dorsal (posterior) root and the most external bundle of the ventral (anterior) root, and into an *anterior column* (Fig. 96, *ant. col.*) between the ventral (anterior) fissure and the most external bundle of the ventral (anterior) root. The part traversed by the bundles of the ventral (anterior) root, as they make for the ventral (anterior) horn, accordingly belongs to the anterior column; but some writers speak of the anterior column as lying between the ventral (anterior) fissure and the nearest bundle of the ventral (anterior) root, thus making the region of the ventral (anterior) root belong to neither anterior nor lateral column. And indeed the distinction between the anterior and the lateral column is to a great extent an artificial distinction.

§ **563**. The 'white matter' consists almost exclusively of medullated fibres supported partly by connective tissue and partly by a peculiar tissue known as *neuroglia*, of which we shall presently speak. The fibres are of various sizes, but many of them are large, and in nearly all of them the medulla is conspicuous. They run for the most part longitudinally, so that in transverse sections of the cord nearly the whole of the white matter appears under the microscope to be composed of minute circles, the transverse sections of the longitudinally disposed fibres, imbedded in the supporting structures. When examined by ordinary modes of preparation these longitudinal medullated fibres of the white matter, though they may occasionally be seen to bifurcate appear, on the whole, to run an undivided unbranched course; but a special mode of preparation has revealed the fact that they give off very fine lateral branches. This method known as that of Golgi, of which there are several modifications, consists in so treating the tissue with a silver salt and other reagents that while the mass of the tissue is rendered clear and transparent the course of the fibres, and especially of the very fine fibres is marked out by black lines consisting of reduced and deposited silver. By this method we learn that the longitudinal fibres of the white matter give off, generally at right angles, exceedingly fine branches, known as *collaterals*, which running transversely pass into the grey matter and there end in a manner to be described. Owing to the relative abundance of the white refractive medulla, the white matter possesses in fresh specimens a characteristic opaque white colour; hence the name. The grey matter from the relative scantiness of medulla has no such opaque whiteness, is much more translucent, and in fresh specimens has a grey or rather pinky grey colour, the reddish tint being due to the presence partly of pigment and partly of blood, for the blood vessels are much more abundant in the grey matter than in the white.

The pia mater which closely invests the cord all round consists of connective tissue, fairly rich in elastic elements and abundantly supplied with blood vessels; it is indeed essentially a vascular membrane and furnishes the nervous elements of the cord with their chief supply of blood. It sends in at intervals partitions or septa of the same nature as itself radiating towards the central grey matter. The narrow dorsal (posterior) fissure is completely filled up by a large septum of this kind, indeed as we have said is in reality a large septum not a fissure; but the ventral (anterior) fissure is too wide for such an arrangement; the whole membrane dips down into this fissure, following the surface of the cord and being reflected at the bottom. From these primary septa, secondary finer septa still composed of ordinary fibrillated connective tissue, carrying blood vessels, branch off; but these are soon merged into the peculiar supporting tissue called, as we have said, neuroglia. This consists in the first place of small branching cells, lying in various planes. The branching is excessive, so that the body of the cell is reduced to very small dimensions, indeed at times almost obliterated, the nucleus disappearing while the numerous branches are continued as long fine filaments or fibres pursuing a devious but for the most part a longitudinal course. In the second place these cells and fibres or filaments are imbedded in a homogeneous ground substance. Relatively to the fibres and ground substance the bodies of the cells (which are called Deiter's cells), especially bodies such as bear obvious nuclei, are very scanty; hence in sections, especially in transverse sections, of the cord the neuroglia has often a dotted or punctated appearance, the dots being the transverse sections of the fine longitudinally disposed fibres imbedded in the ground substance. Examined chemically the neuroglia is found to be composed not like connective tissue of gelatine, but of a substance which appears to be closely allied to keratin, the chief constituent of horny epidermis, hairs and the like, § 435, and which has therefore been called *neurokeratin*, (see also § 68). And indeed this neuroglia, though like connective tissue a supporting structure, is not, like connective tissue, of mesoblastic, but of epiblastic origin. The walls of the neural canal of the embryo which are transformed into the spinal cord of the adult consist at first of epithelial, epiblastic cells; and while some of these cells become nervous elements, others become neuroglia. The epithelial cells which are destined to form neuroglia become exceedingly branched, while their originally protoplasmic cell-substance becomes transformed to a large extent into neurokeratin.

The neuroglia fills up the spaces between the radiating larger septal prolongations of the pia mater and the finer branched septa which starting from the larger ones carry minute blood vessels into the interior of the white matter. In these spaces it is so arranged as to form delicate tubular canals, of very variable size, running for the most part in a longitudinal direction. Each of these tubular canals is occupied by and wholly filled up with a medullated nerve fibre of corresponding size. A medullated nerve fibre of the white matter of the spinal cord resembles a medullated nerve fibre of a nerve (§ 68) in being composed of an axis-cylinder and a medulla; but it possesses no primitive sheath or neurilemma. This is absent and indeed is not wanted; the tubular sheath of neuroglia affords in the spinal cord (and as we shall see in the central nervous system generally) the support which in a nerve is afforded by the neurilemma. Nodes are, according to most authors, absent, but some say they are present.

The white matter of the cord consists then of a more or less solid mass of neuroglia, having the structure just described, which is permeated by minute canals, some exceedingly fine and carrying very fine fibres, 2μ or even less, others larger and carrying fibres up to the size of 15μ or even more. This mass is further broken up into areas by the smaller and larger vascular connective-tissue septa with the edges and endings of which the neuroglia is continuous. Most of the nerve-fibres, as we have said, run longitudinally and in a transverse section of the cord are cut transversely; as we shall see fibres, more especially very fine fibres and in particular 'collateral' fibres, are continually passing into and out of the white matter, and in so doing take a more or less transverse course; but by far the great majority of the readily visible fibres, and the neuroglia canals in which these lie run in a longitudinal direction. On the outside of the cord below the pia mater the neuroglia is developed into a layer of some thickness from which nerve fibres are absent; this is often spoken of as an inner layer of the pia mater; but being neuroglia and not connective tissue is of a different nature from the pia mater proper. A layer of this superficial neuroglia also accompanies the larger septa, and a considerable quantity is present in the large septum called the dorsal fissure.

The pia mater carries not only blood vessels but also lymphatics; of these however we shall speak when we come to deal with the vascular arrangements of the whole of the central nervous system.

§ **564**. In the grey matter we may distinguish the larger, more conspicuous nerve-cells and the rest of the grey matter in which these cells lie. We have already (§ 99) described some of the general features of these nerve-cells; but they must now be dealt with in greater detail. Our knowledge of the characters of these cells has of late years been greatly extended by the application of the silver method of Golgi and also of the methylene-blue method. When methylene-blue is injected into a living animal, certain cells take up and are stained by the colouring matter, and by this means are clearly marked out from the other elements of the tissues which do not so stain. Among the cells which so stain, are the cells of the central nervous system. It is necessary for the reaction that the cells should be living; they do not take up the methylene-blue and do not stain in the same way when they are dead. The silver method and the methylene-blue method applied to the central nervous system give very concordant results and have led to the following conclusions concerning the features of the nerve-cells belonging to it.

The body of each cell (Fig. 97) is prolonged into processes of two kinds. The one kind of process, and in at least the vast majority of cells only one such process is present, becomes the axis-cylinder of a nerve-fibre and is spoken of as the axis-cylinder process; it has also been called the *neuraxon* or the *axon*. As a rule this kind of process runs a long course without dividing, though while within the central nervous system it may give off collaterals; but in some instances it may divide into a large number of branches at no great distance from the body of the cells of which it is a process. A typical axon is that of one of the cells in the ventral horn, which becoming the axis-cylinder of one of the fibres of the ventral root runs an undivided course until it reaches a skeletal muscle, in which after some division, it ends in certain end-plates of the muscle.

The other kind of process, and a cell usually has several such, divides very rapidly, at no great distance from the nucleus of the cell, in a dendritic fashion, into a number of fine branches which appear to end abruptly, without becoming actually continuous with any other structures. It has been suggested that the processes of this kind do not carry out nervous actions but serve simply for the nourishment of the cell; hence they have been by some called *protoplasmic processes*. But there is no real foundation for this view; the evidence is distinctly in favour of their taking a share in nervous actions, and it is better to adopt another term which has been used, *dendritic processes* or, shortly, *dendrites*. Hence a typical nerve cell of the central nervous system may be described as consisting of a body surrounding the nucleus and prolonged into processes of which one is the axis-cylinder process, neuraxon, axon, and the others are dendrites. It will be convenient to distinguish by a separate name between the processes whether axon or dendrite, and the part from which these processes start, namely the body of the cell surrounding the nucleus; the latter might be called the *perikaryon*[1].

The axon if it leaves the spinal cord ends in one or more end-plates or in other terminal organs. If, as is the case with a large number of cells, the axon continues to run and finally ends in the central nervous system, its mode of termination as well as that of the collaterals to which it may give rise is in the form of an arborescent tuft, which is applied to the body or dendrites of some other cell. So far as our present knowledge goes we are led to think that the tip of a twig of the arborescence is not continuous with but merely in contact with the substance of the dendrite or cell-body on which it impinges. Such a special connection of one nerve-cell with another might be called a *synapsis*[1].

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[1] περι and καρυον nucleus.

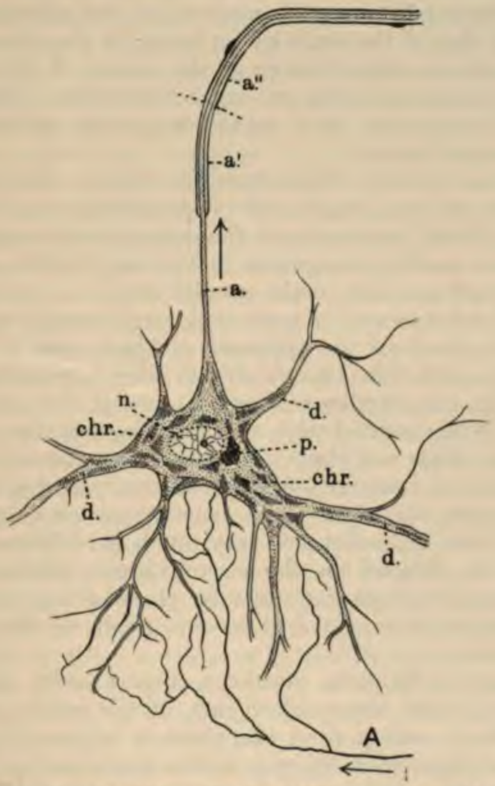

FIG. 97. DIAGRAM OF A NEURON WITH PERIKARYON, DENDRITES (*d.d.d.*) AND AXON.

The perikaryon contains nucleus (*n*), pigment (*p*) and chromatic substance (*chr*). Note the absence of the latter from the axon. The axon acquires a myelin sheath (a'), then, outside the cord, a primitive sheath (a'').

A, is the termination of the axon of another cell approaching close to the perikaryon and dendrites of the neuron figured.

There are reasons for believing, though the matter is not one definitely proved, that in the ordinary action of the cell, nervous impulses pass along the axon centrifugally from the cell, and along the dendrites centripetally to the body of the cell surrounding the nucleus. Hence we may suppose that nervous impulses or influences sweeping along the axon of one cell are brought to bear through the terminal arborisation of the axon or that of a collateral, on the dendrites of another cell, setting up in those dendrites nervous changes, which passing to the body of that cell issue in turn along its axon. And it has been suggested that the lack of continuity between the material of the arborisation of the one cell and that of the dendrite (or body) of the other cell offers an opportunity for some change in the nature of the nervous influence as it passes from the one cell to the other. But this must be regarded at present as a useful suggestion rather than as a definitely proved truth.

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[1] From σύν and ἅπτω clasp.

So far as we know, these features, namely the possession of an axon on the one hand and of dendrites on the other, are common to all the nerve-cells of the central nervous system; they may be more readily recognised in the larger, more conspicuous cells but are present also in the smaller ones.

The cell-substance of a nerve-cell, large enough to be studied conveniently, presents an appearance which may be spoken of under the general term 'granular'; it often however bears marks of fibrillation, the fibrillæ seeming to sweep into or out of the processes. When treated with staining reagents the whole of the cell-substance does not stain alike; there are usually in the cells different kinds of material, staining differently, and sometimes this is conspicuously the case. The exact appearances and staining reactions of the cell-substance vary much in different specimens and appear to depend on the circumstances affecting the cell. Among these circumstances must be placed the previous activity or quiescence of the cell; but to this point we shall return in another place.

Such nerve-cells form, however, a part only, and in most regions of the cord the smaller part, of the whole grey matter. In a transverse section from the thoracic region (Fig. 96) a few only of these nerve-cells are seen in the whole section, and though they appear more numerous in sections from the cervical and especially from the lumbar regions (Figs. 99, 100), yet in all cases they occupy the smaller part of the area of the grey matter. The larger part of the grey matter consists, besides a neuroglia supporting the nervous elements, of nerve filaments running in various directions and forming, not a plexus properly so called, but an interlacement of extreme complexity. The constituents of this nervous tangle as seen in a transverse section may be briefly described as follows. It consists in part of the terminal portions of the dendrites of nerve-cells; these cannot in a section be traced distinctly very far from the body of the cell, they are lost to view in the tangle. It will be understood of course that in a section a large part of this constituent of the grey matter will belong to cells whose bodies are not seen in the section, since these lie either above or below the plane of the section, their dendrites alone, and only some of these passing into the section. To these terminal portions of dendrites of nerve-cells are attached the terminal arborisations of certain axons, belonging to cells which as we have said may be a long way off. These dendrites and the arborisations in contact with them both form as it were the basis of the tangle of grey matter; but they form only a part and indeed a small part of it. To this we must add a number of naked axis-cylinders, axons, of various sizes, some large, some quite small, running in various directions; of these some are about to end immediately in arborisations, others are simply sweeping through the portion of grey matter under view, on their way to some other part of the grey matter or to the white matter. The above are all non-medullated nervous elements. There are also present, in relatively large numbers, the particular fine medullated fibres of which we spoke above; of these, which also run in various directions, some are collaterals, and while some are soon about to end, losing their scanty medulla, in arborisations lying in the section, or close to it, others are on their way to other, it may be, distant connections. Lastly there are present a certain number of ordinary medullated fibres, some of even large size; these running also in various directions may be considered as simply passing through the grey matter under view on their way to other parts. All these several elements, some being terminal and forming a basis, others coming in to end in that basis, and yet others simply passing through it on their way elsewhere, all intricately interwoven, all supported in a bed of neuroglia, make up with the obvious well-defined nerve-cells what we call the grey matter. It should be added that besides the nerve-cells spoken of above, which, though of various sizes, are all large enough for their features to be readily recognized, a number of other cells of very small size, some of which at all events must be regarded as true nerve-cells, are present in the grey matter.

The neuroglia in which all these structures, nerve-cells, fine medullated nerve-fibres, naked axis-cylinders and fine filaments, are imbedded is identical in its general characters with that of the white matter, but, as naturally follows from the nature of the nervous elements which it supports, is differently arranged. Instead of forming a system of tubular channels it takes on the form of a sponge-work with large spaces for the larger nerve-cells and fine passages for the nervous filaments. At the junction of the grey matter with the white matter, the neuroglia of the one is continuous with that of the other, and the connective-tissue septa of the latter run right into the former; the outline of the grey matter is not smooth and even, but broken by tooth-like processes due to the septa. Since, as we have just said, some of the true nerve-cells are very small, and since the nerve filaments like the neuroglia fibres are very fine and take like them an irregular course, it often becomes very difficult in a section to determine exactly which is neuroglia and which are nervous elements. The neuroglia cells may however be distinguished perhaps from the smaller nerve-cells by their nuclei not being so conspicuous or so relatively large as in a nerve-cell, and by their staining differently.

The grey matter then may be broadly described as a bed of neuroglia, containing a certain number of branching nerve-cells, for the most part though not exclusively large and conspicuous, but chiefly occupied by what is not so much a plexus as an intricate interweaving of nerve filaments running apparently in all directions. It may be added that the grey matter is well supplied with blood vessels, these being in it, as stated above, relatively much more numerous than in the white matter.

§ **565.** The central canal is lined by a single layer of columnar epithelial cells, which are generally described as bearing cilia; but it is not certain that the processes which may be seen projecting from the surfaces of the cells are really cilia. These epithelial cells rest not on a distinct basement membrane but on a bed of neuroglia, free apparently or nearly so from nervous elements, which surrounds the central canal and is sometimes spoken of as the *substantia gelatinosa centralis* (Fig. 96, *c. g. s.*). The attached bases of the epithelial cells are branched or taper to a filament, and become continuous with the branched cells or fibres of the neuroglia below. As we said above the neuroglia elements are transformed epithelial cells; and the continuity of the cells, which retaining the characters of epithelial cells form a lining to the canal, with the cells which have become branched and lost their epithelial characters indicates the epithelial origin of the latter.

The central canal with the surrounding area of neuroglia forms the central part of the isthmus uniting the two lateral halves of the cord. Dorsal (posterior) to this central mass lies the *posterior grey commissure* (Figs. 96, *p. g. c.*, 99, 100), composed chiefly of fine filaments running transversely, and ventral (anterior) to it lies first the thinner *anterior grey commissure* (Figs. 96, *a. g. c.*, 99, 100) of a similar nature, and then the relatively thick *white commissure* (Figs. 96, *a. c.*, 99, 100) which is formed by medullated fibres crossing over from one side of the cord to the other, and thus constitutes a decussation of fibres along the whole length of the cord. On each side, the central mass of neuroglia of which we are speaking gradually merges into the central grey matter of the corresponding lateral half.

The end or head (caput) as it is frequently called of the dorsal, posterior horn is occupied not by ordinary grey matter, but by a peculiar tissue, the *substantia gelatinosa of Rolando*, which forms a sort of cap to the more ordinary grey matter differing in size and shape in different regions of the cord. Cf. Figs. 96, 99, 100 *s.g.* In carmine and some other modes of preparation it is frequently stained more deeply than is the ordinary grey matter, and in such preparations is very conspicuous. It may be described as consisting of a somewhat peculiar neuroglia traversed by fibres of the dorsal, posterior root, and containing a large number of cells, which, for the most part small, the cell-bodies being small relatively to the nuclei, are not all alike, some being probably nervous and others not. It takes origin from the cells forming the immediate walls of the embryonic medullary canal. In the embryo, this canal is relatively wide, though compressed from side to side, and in transverse sections of the medullary tube appears at a certain stage as a narrow oval slit placed vertically, and reaching almost from the dorsal to the ventral surface. The dorsal part of this long slit is later on closed up by the coming together of the walls and the obliteration of the greater part of the cavity, leaving the ventral part to form a circular canal, which by the development of the ventral columns assumes the central position. During this closure of the dorsal part of the canal a mass of the cells lining the canal is cut from the rest on each side, and during the subsequent growth takes up a position at the end of the dorsal horn. Hence, though it never apparently contains any cavity, the substance of Rolando may be regarded as an isolated portion of the walls of the medullary canal, which has undergone a development somewhat different from that of the portion which remains as the lining of the central canal. Traces of this origin may be seen even in the adult. Thus in the lower end of the cord, in what we shall speak of presently as the *conus medullaris*, the central canal widens out dorsally, and in section (Fig. 98, *A*) presents on each side a bay *x*, stretching out towards the position of the dorsal horn. At this region of the cord, though both white and grey matter are developed on the ventral surface, the posterior columns

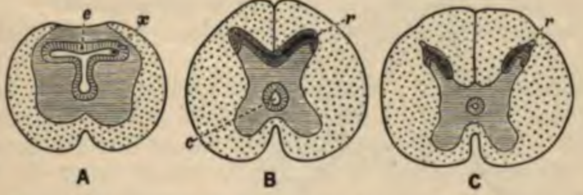


FIG. 98. DIAGRAM TO ILLUSTRATE THE NATURE OF THE SUBSTANCE OF ROLANDO.

The figures are purely diagrammatic and are not drawn to the same scale. In all three figures the grey matter is shaded with fine lines and the white matter with dots.

A. transverse section of the lower end of the conus medullaris in man. *e*. epithelium lining the medullary canal. *x*. lateral expansion of the canal.

B. transverse section of the spinal cord of the calf in the lower thoracic region. *r*. substance of Rolando. *c*. central canal.

C. transverse section through mid thoracic region of cord in man. *r*. substance of Rolando.

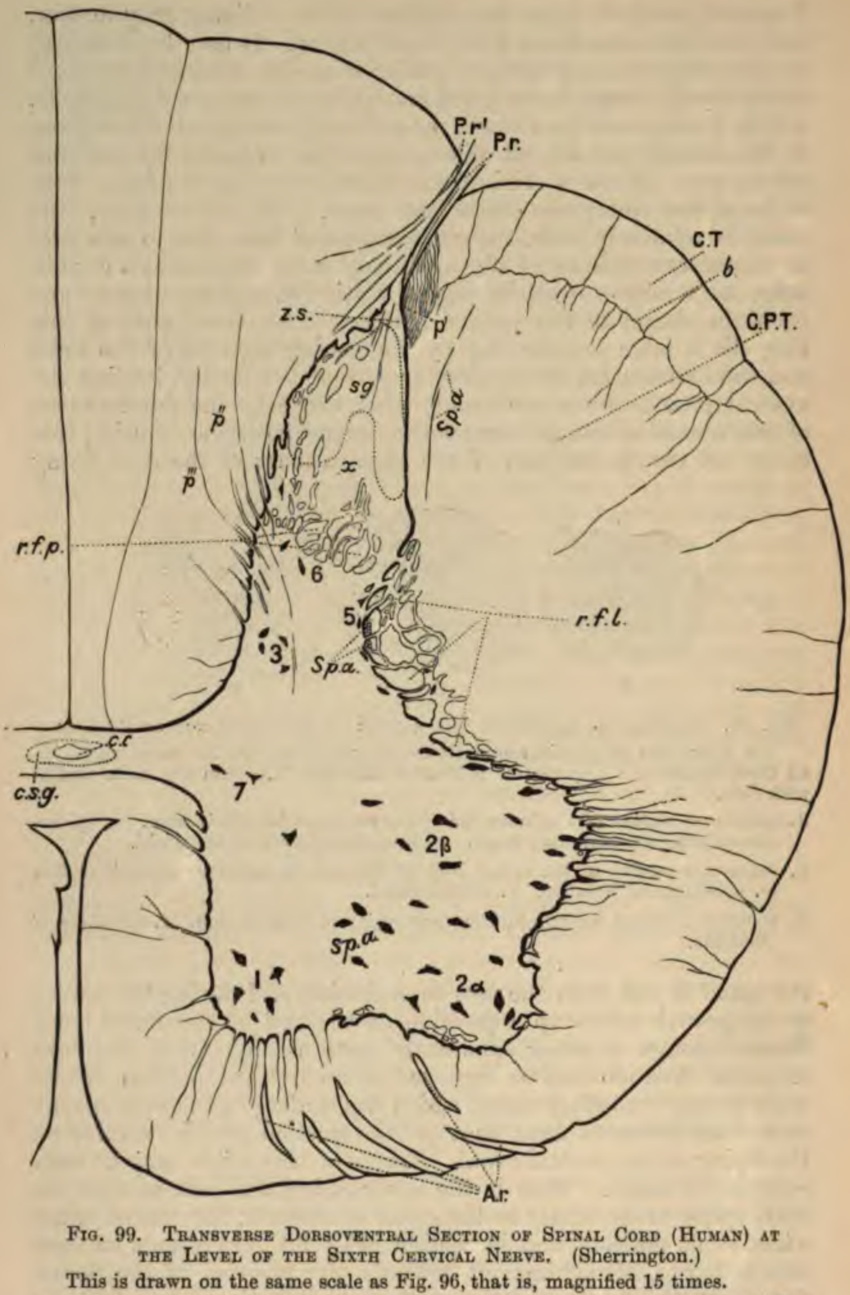


Fig. 99. Transverse Dorsoventral Section of Spinal Cord (Human) at the Level of the Sixth Cervical Nerve. (Sherrington.)

This is drawn on the same scale as Fig. 96, that is, magnified 15 times.

r. f. l. lateral reticular formation. *r. f. p.* posterior reticular formation. *p'*. fine fibres of lateral bundle of the posterior root; *p''*, *p'''* fibres of median bundle of posterior root, entering grey matter from external posterior column. *x.* grey matter of posterior horn. *Sp. a.* bundles of fibres belonging to the spinal accessory nerve and issuing from the cell-group in the ventral horn marked *Sp. a.*; in the lateral reticular formation they are seen cut transversely. *b.* is a natural septum of connective tissue marking out the cerebellar tract *C.T.* from the crossed pyramidal tract *C.P.T.* *z. s.* zona spongiosa. 2 *a*, *β*, lateral cells of the anterior horn. 5. Cells in the region of the lateral reticular formation. The other letters of reference are the same as in Fig. 96.

do not meet on the dorsal surface, but leave the central canal covered only by tissue which perhaps may be called neuroglia, but is of peculiar nature and origin. In the calf, in a part of the thoracic region the substance of Rolando is not confined to the tip of the dorsal, posterior horn, but is continued to meet its fellow in the middle line. Fig. 98, *B.* If we imagine the dorsal portion of the canal of *A* to be cut off from the ventral portion, its cavity to be obliterated, and the lining epithelium with some of the surrounding elements to undergo a special development, the condition in *B* is reached by the growth of the posterior columns. From *B*, the transition to the normal state of things as in 98, *C*, is a very slight one. The extreme dorsal tip of the horn being of a more open texture than the substance of Rolando is sometimes called the *zona spongiosa*.

§ **566.** *The grouping of the nerve-cells.* The nerve-cells, at all events the cells which are large enough to be easily and without doubt recognized to be nerve-cells, form, as we have seen, only a part of the grey matter, and in some parts of the cord, in the thoracic region for instance, are so sparse that in a section of the spinal cord in this region thin enough to shew its histological features satisfactorily, the bodies of a few only of such cells are visible (Fig. 96); the greater part of the grey matter consists not of the bodies of conspicuous nerve-cells, but of a mass of fibres and fibrils passing apparently in all directions. In the cervical (Fig. 99) and especially in the lumbar (Fig. 100) regions the nerve-cells are both absolutely and relatively more abundant; but even in a section taken from the lumbar region the nerve-cells, all put together, form the smaller part of the whole area of grey matter. Moreover, in respect of the number of cells all the sections of even the same region of the cord are not alike. Seeing that the cord may be considered as growing out of the fusion of a series of paired ganglia, each ganglion corresponding to a nerve, cf. § 96, we may fairly expect to find the fusion not complete, so that the nerve-cells would appear more numerous opposite a nerve than in the middle between two nerves. In some of the lower animals this arrangement is most obvious, and there are some reasons for thinking that even in man the nerve-cells are metamerically increased at the level of each nerve.

Even when casually observed it is obvious that the nerve-cells are not scattered in a wholly irregular manner throughout the grey matter, being for instance much more conspicuous in the ventral horn than elsewhere; and more careful observation allows us to arrange them to a certain extent in groups.

The cells of the ventral horn are for the most part large and conspicuous, 67μ to 135μ in diameter, branch out in various directions, and present an irregular outline in sections taken in different planes. We have reason to think that every one of them possesses an axis-cylinder process which, in the case at all events of most of the cells, passing out of the grey matter becomes a fibre of the adjacent anterior root. They are obvious and conspicuous in all regions of the cord, though much more numerous and individually larger in the cervical and lumbar enlargements than in the thoracic region. We may further, with greater or less success, divide them into separate groups.

In the cervical and lumbar regions a fairly distinct group of cells is seen lying on the median side of the grey matter close to the anterior column (Figs. 99, 100, **1**). This may be called *the median group.* It appears also in the thoracic region (Fig. 96, **1**); indeed the question arises whether all the cells of the ventral horn in this region do not belong to this group. The other cells so conspicuous in the lumbar and cervical enlargements, and therefore probably in some way associated with the limbs, may be spoken of as forming altogether a *lateral group* or *limb group;* but we may, though with some uncertainty, subdivide them into two or three groups. Thus in the lumbar region a group of cells (Fig. 99, **2**γ) lying near the lateral margin of the more dorsal part or base of the horn may be distinguished, as a *dorso-lateral subgroup,* from the cells occupying the ventral lateral corner of the horn and forming a *ventro-lateral subgroup* (Fig. 100, **2**β); and the same distinction, though with less success, may be made in the cervical region (Fig. 99). Further, we may perhaps in both regions distinguish a group of cells placed in the lumbar region in the middle of the horn as a *central subgroup* (Figs. 99, 100, **2**α). But, in all cases, the separation of these cells, which we have spoken of as a whole as lateral cells, into minor groups, is far less distinct than the separation of the median group from these lateral cells, especially if we admit that in the thoracic region, the median group is alone clearly represented.

In the thoracic region a group of rather smaller cells is seen at the base of the anterior horn, near to the junction with the isthmus (Fig. 96, **7**). In the cervical and lumbar region these cells are very scanty (Figs. 99, 100, **7**).

The cells of the dorsal horn contrast strongly with those of the anterior horn in being few, and for the most part small. They are branched; and, like the cells of the ventral horn, each possesses an axis-cylinder process, though this is not easily determined without special preparation; the processes do not run out to join the dorsal root as do the corresponding processes in the ventral horn and therefore are not so readily seen. These cells occur in all regions of the cord, and appear to be arranged into two more groups. The lateral margin of the dorsal horn, at about the middle or neck of the horn, is along the whole length of the

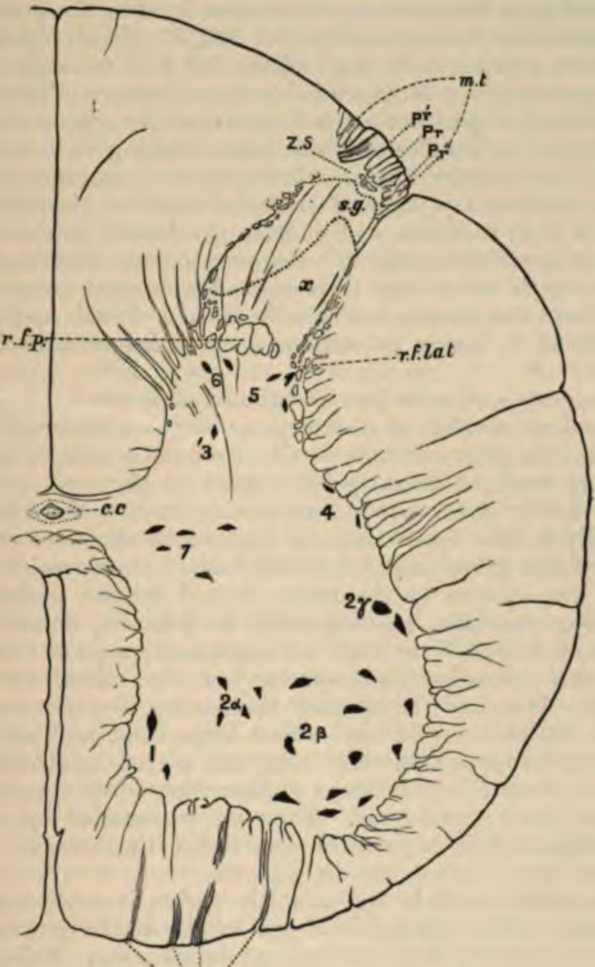


FIG. 100. TRANSVERSE DORSOVENTRAL SECTION OF THE SPINAL CORD (HUMAN) AT THE LEVEL OF THE THIRD LUMBAR NERVE. (Sherrington.)

This is drawn to the same scale as Figs. 96, 99 and in the same way except that the outline of the grey matter is not exaggerated. *Pr'*. median, *Pr*. intermediate, *Pr''*. lateral bundles of posterior roots. The region comprised under *m.t.* is the marginal zone or Lissauer's zone. The other letters of reference are the same as in 96 and 99.

The three figures 96, 99, 100 are intended to illustrate the main differential features of the thoracic, cervical, and lumbar cord.

cord, but especially in the cervical region, much broken up by bundles of fibres passing in various directions and forming an open network, called the *lateral reticular formation* (Figs. 99, 100, *r. f. lat.*). In all regions of the cord a number of cells are found associated with this reticular formation, forming *the group of the lateral reticular formation* (Figs. 99, 100, **5**). In all regions of the cord also a group of cells (Figs. 96, 99, 100, **6**) is found in that part of the horn where, a little ventral to the substance of Rolando, the uniform field of grey matter is broken up into a kind of network by a number of bundles of white fibres running in various directions. This network has also been called a reticular formation, and has received the name of *posterior reticular formation* (Figs. 98, 99, *r. f. p.*) to distinguish it from the lateral reticular formation just mentioned; the two however in some regions (see Fig. 96) join each other, and thus cut off a ventral portion of the dorsal horn containing nerve-cells from a dorsal portion, *x* in Figs. 98, 99, in which no obvious or conspicuous nerve-cells are present.

The groups of cells just mentioned with the restrictions and modifications spoken of occur along the whole length of the cord; but the group of cells to which we must now call attention is almost confined to a special region of the cord, or at least is but feebly represented elsewhere. In the thoracic region, especially in the lower thoracic region (we shall return to the limits of the group later on) at the base of the dorsal horn (Fig. 96, **3**) just ventral to the curve formed by the posterior grey commissure as this bends dorsally to join the dorsal horn, is seen on each side of the cord a conspicuous group of cells known as *Clarke's column* or the *posterior vesicular column* or *vesicular cylinder*. The cells composing this group, though varying in size at different levels, are rather large cells, and are for the most part fusiform, with their long axis placed lengthways along the cord, so that in transverse sections they often appear to have a rather small round body. They are surrounded by and as it were imbedded in a mass of fine fibres, the area of which is indicated by a dotted line in Fig. 96.

Also conspicuous in the thoracic region is another group of cells lying on the outer side of the middle of the grey matter at about the junction of the ventral and dorsal horns. This is known as the *intermedio-lateral tract* and is sometimes called the *lateral horn* (Fig. 96, **4**). The cells composing it are somewhat small spindle-shaped cells with their long axis placed transversely. The group is conspicuous as we have said in the thoracic regions; it may be recognized in the lumbar region (Fig. 100, **4**), but in the cervical region becomes confused with the most dorsally placed or lateral subgroup of the ventral horn. We shall however have to return to these groups of cells when we come to speak of the differences between the several regions of the cord.

§ 567. *The tracts of white matter.* At first sight the white matter of the cord appears to be of uniform nature. We can use the nerve roots to delimitate the anterior, posterior and lateral columns, but we appear to have no criteria to distinguish parts in each column. In the cervical and upper thoracic regions of the cord, a septum (Fig. 96, *s.*) in the posterior column, somewhat more conspicuous than the other septa, has enabled anatomists to distinguish an inner median portion, the *median posterior column*, commonly called the *postero-median column* or *column of Goll* (Fig. 96, *m. p.*), from an outer lateral portion, the *external posterior column*, commonly called the *postero-external column* or *column of Burdach* (Fig. 96, *e. p.*), the lateral part of which, nearer the grey matter, has, for reasons which we shall see later on, been called the *posterior root-zone.* But beyond this neither the irregular septa nor other features will enable us to distinguish one part of the white matter as different in nature from another. Nor have we better success when with the scalpel we attempt to unravel out the white matter into separate strands. Nevertheless we have convincing evidence that the white matter is arranged in strands, or tracts, or columns, which have different connections at their respective ends, which behave differently under different circumstances, which we have every reason to believe carry out different functions, but which cannot be separated by the scalpel because each of them is more or less mixed with fibres of a different nature and origin. The evidence for the existence of these tracts is twofold.

One kind of evidence is embryological in nature. When a nerve fibre is being formed in the embryo, either in the spinal cord or elsewhere, the essential axis-cylinder is formed first and the less essential medulla is formed later. Now when the developmental history of the spinal cord is studied it is found that, in the several regions of the cord, all the fibres of the white matter do not put on the medulla at the same time. On the contrary, in certain tracts, the medulla of the fibres makes its appearance early, in others later. By this method it becomes possible to distinguish certain tracts from others.

Another kind of evidence is supplied by facts relating to the degeneration of the fibres of the white matter. We have seen (§ 561) that the degeneration of a nerve fibre is the result of the separation of the fibre from its trophic centre, and that while the trophic centre of the afferent fibres is in the ganglion on the posterior root, that of the efferent fibres is in some part of the spinal cord. In the case of the efferent fibres the degeneration might be spoken of as *descending* from the spinal cord to the muscles or other peripheral organs. In the case of the afferent fibres of the trunk of the nerve, the degeneration is also one descending from the ganglion down to the skin or other peripheral organ. When however the section is carried through the posterior root of a spinal nerve, the degeneration takes place in the part of the nerve between the section and the spinal cord, it runs up from the section to and into the spinal cord, and may therefore be called an *ascending* degeneration. Thus we may say that when a nerve trunk or when a nerve root is cut completely across, all the fibres which are thereby separated from their trophic centres degenerate. When the nerve trunk is divided all the fibres below the section undergo descending degeneration. If the ventral root be cut across, all the fibres of the root below the section undergo descending degeneration. If the dorsal root be cut across, all the fibres of the root above the section undergo ascending degeneration with the exception of certain fibres which do not degenerate at all, and of which we shall speak later on.

When the spinal cord is cut across, for instance in the thoracic region, all the fibres of the white matter do not degenerate either in the part of the cord above the section or in the part below. Some fibres, and indeed some tracts of fibres degenerate, and some do not. Further, some tracts degenerate in the cord above the section, and thus undergo what has been called an ascending degeneration; other tracts degenerate in the cord below the section, and thus undergo what has been called a descending degeneration. These terms must however be used with caution. When a nerve trunk is cut across, the degeneration actually descends, in the sense that the progress of the degenerative changes may be traced downwards; they begin at the section and travel downwards at a rate sufficiently slow to permit a difference being observed between the progress of degeneration at a spot near the section and that at one farther off. After section of or injury to the spinal cord, however, it is not possible to trace any such progress either upwards or downwards; in the tracts both above and below the section or injury, degeneration either begins simultaneously along the whole length of the degenerating tract, or progresses along the tract so rapidly that no differences can be observed as far as the stage of degeneration is concerned between parts near to and those far from the section or injury. When, for instance, the cord is divided in the cervical region, subsequent examination of the tracts of so-called descending degeneration shews that the degeneration is as far advanced in the lumbar region far away from the section as in the cervical region just below the section. Applied to the spinal cord, therefore, the term descending degeneration means simply degeneration below the seat of injury or disease, ascending degeneration means simply degeneration above the seat of injury or disease. We may add that the histological features of the degeneration of fibres in the spinal cord are not wholly identical with those of the degeneration of fibres in a nerve trunk. Thus, the neurilemma with its nuclei being absent from the fibres of the cord, no proliferation of nuclei takes place; the axis-cylinder and medulla simply break up, are absorbed and disappear.

Similar degenerations, ascending, or descending, or both, are seen when the section is not carried right through the whole cord, but particular parts of the cord are cut through or simply injured. And similar degenerations occur as the consequences of disease set up in parts of the cord.

In this way the results of sections of or of other injuries to or of diseases of the spinal cord have enabled us to mark out certain tracts of the white matter as undergoing degeneration and others as not, and moreover certain tracts as undergoing descending and others as undergoing ascending degeneration. Further, the delimitation of tracts of white matter by the process of degeneration agrees so well with the results of the embryological method as to leave no doubt that the white matter does consist of tracts which differ from each other in nature and in function.

The several tracts thus indicated vary in different regions of the cord. They may be broadly described as follows.

I. *Descending tracts*, that is to say, tracts which undergo a descending degeneration in the sense noted above.

The most important and conspicuous is a large tract (Fig. 101, *cr. P.*) occupying the posterior part of the lateral column, coming close upon the outer margin of the dorsal horn, and for the most part not reaching the surface of the cord. We shall have to return to this tract more than once, and may here simply say that it may be traced along the whole length of the cord from the top of the cervical region to the end of the sacral region, that it may be also traced right through the brain and indeed begins at the surface of the cerebral hemispheres, and that it enters the cord from the brain through the structures called the pyramids of the bulb, which we shall study later on. These pyramids cross over or decussate as they are about to pass into the cord, forming what is known as the decussation of the pyramids, and the tract of fibres in question shares in this decussation. Hence this tract is called the *crossed pyramidal tract* or more simply the *pyramidal tract*.

It is no less distinctly marked out by the embryological method. The fibres forming this tract acquire their medulla later than do all other fibres of the cord; in the human embryo the medulla does not appear in them until about the end of the ninth month. See Fig. 102.

A smaller, less conspicuous descending tract occupies the median portion of the anterior column (Fig. 100, *d. P.*). This is not only much smaller but also much more variable than the crossed pyramidal tract, is not present in the lower animals, being found in man and the monkey only and being better developed in man than in the monkey, and reaches a certain way only down the spinal cord, generally coming to an end in the thoracic region. It too comes down from the pyramid, and is a continuation of that part of the pyramid which unlike the rest does not decussate in the bulb; thus the tract which coming down from the left side of the brain runs in the left pyramid in the bulb, passes down into the left anterior column of the cord. Hence this smaller tract is called the *direct pyramidal tract.*

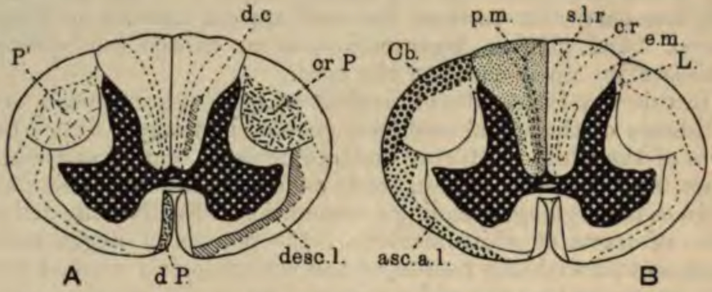


Fig. 101. Diagram to illustrate the general arrangement of the several Tracts of White Matter in the Spinal Cord.

The section is taken at the level of the fifth cervical nerve. The relations of the tracts in different regions of the cord are shewn in Fig. 107.

The descending tracts, tracts of descending degeneration, are shaded with lines (figure A); the ascending tracts, tracts of ascending degeneration, are shaded with dots (figure B).

cr.P. crossed pyramidal tract, or more shortly pyramidal tract. *d.P.* direct pyramidal tract, shaded on the side opposite to that on which *cr.P.* is shaded, in order to indicate the difference of the two as to crossing. *P'*, idiolateral degeneration in pyramidal tract. *desc.l.* the antero-lateral descending tract. The area, shaded, and marked *d.c.* in A, but left unshaded in B, is the small descending tract or rather patch mentioned in the text as observed, in certain regions of the cord, in the external posterior column *e.m.* *C.b.* cerebellar tract. *p.m.* or *s.lr.* and *c.r.* together indicate the median posterior tract or tract of fibres of the dorsal roots, *c.r.* representing, as is explained more fully in the text, the brachial and *s.lr.* the sacral, lumbar and thoracic roots. *asc.a.l.* the antero-lateral ascending tract. The small area at the tip of the posterior horn, marked *L*, is the posterior marginal zone or Lissauer's zone.

Moreover it has been observed that an injury, which gives rise to descending degeneration in the crossed and direct pyramidal tracts, for instance a lesion of one cerebral hemisphere, also causes descending degeneration in a number of scattered fibres which lie within an area having the same situation as that of the crossed pyramidal tract in the lateral column except that it is not on the crossed side, *contralateral*, but like the direct pyramidal tract on the same side, *idiolateral* (Fig. 101, *p'*). Hence what we may in its entirety call 'the great pyramidal tract' as it passes from the brain to the spinal cord divides at the pyramids into three parts. One part, and that by far the greater part, crosses over to the other side, takes a contralateral course, and becomes the crossed (lateral) pyramidal tract, a second smaller part remains on the same side, takes an idiolateral course and becomes the direct (ventral) pyramidal tract, while the remaining third also takes an idiolateral course, but runs in the lateral column and becomes the uncrossed lateral pyramidal tract, the fibres composing it being scanty and scattered.

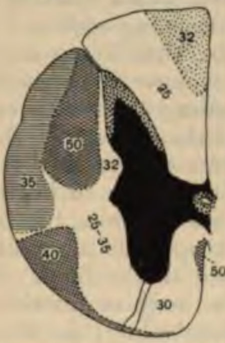


FIG. 102. DIAGRAM SHEWING THE TRACTS IN THE HUMAN SPINAL WHITE MATTER AS REVEALED BY THE DATE OF MYELINATION OF THE NERVE FIBRES.

The numbers indicate the length of the embryo in centimeters at the date of myelination of the tract on which each number is placed. The earliest tracts to develope are left white; the latest, the pyramidal, is darkest (50) and its myelination only occurs after birth. Spongy and gelatinous grey matter are represented by black and stippled fields respectively. It will be noted that if figures A and B in Fig. 103 are combined the area of scantiest degeneration in the combined figure resembles a good deal the area left white in this figure, because short paths develope earliest.

The pyramidal tract is the most conspicuous and important descending tract, but names have been given to two other descending tracts. One, known as the *antero-lateral descending tract*, is a large tract placed in the antero-lateral column, and seen in section (Fig. 101, *desc. l.*) as an elongated area stretching from the pyramidal tract towards the anterior column and reaching at times as far as the ventral fissure. The area is large, however, because the tract is very diffuse, that is to say, the fibres with descending degeneration, or fibres which degenerate below the section or injury, are very largely mixed up with fibres which do not so degenerate; in this respect this tract contrasts with the crossed pyramidal tract, which is to a much greater extent composed of fibres with descending degeneration, though even in it there are a considerable number of fibres which do not degenerate. Indeed this antero-lateral descending tract is so diffuse that it hardly deserves to be called a tract.

The other is a small, narrow, comma-shaped tract (Fig. 101, *x*), situated in the middle of the external posterior column but limited to the cervical and upper thoracic regions, and has been called the "descending comma tract." But the degeneration reaches a short way only below the section or injury, and the group of fibres thus degenerating can hardly be considered as forming a tract comparable to the other tracts. The area is in part composed of the descending portions of certain fibres of the dorsal root, which, as we shall see, divide soon after entering the cord, into an ascending and a descending portion. But it contains also fibres which, starting from cells lying within the cord itself, take a descending course.

II. *Ascending tracts*, that is to say, tracts in which the degeneration takes place above the section or injury.

A conspicuous ascending tract of a curved shape (Fig. 101, *C. b.*) occupies the outer dorsal part of the lateral column lying to the outside of the crossed pyramidal tract, between it and the surface of the cord. It appears to begin in the upper lumbar region, being said to be absent from the lower lumbar and sacral cord, and may be traced upwards increasing in size through the thoracic and cervical cord to the bulb. In the bulb it may be traced into the restiform body or inferior peduncle of the cerebellum, and so to the cerebellum; for the restiform body serves, as we shall see, in each lateral half of the brain, as the main connection of the cerebellum with the bulb and spinal cord. Hence this tract is called *the cerebellar tract* or sometimes the *direct cerebellar tract*. The medulla appears in the fibres of this tract at about the beginning of the seventh month.

A second important ascending tract occupies the median portion of the posterior columns (Fig. 101, *c.r.*, *s.lr.*), and so far coincides with what we described above as the median posterior column, in the upper regions of the cord, that it may be called the *median posterior tract*; it extends along the whole length of the spinal cord, varying at different levels in a manner which we shall presently study, and ending above in the bulb.

A third ascending tract, called the *ascending antero-lateral tract*, or tract of Gowers, occupies (Fig. 101, *asc. a. l.*) the outer ventral part of the lateral column. It has somewhat the form of a comma, with the head filling up the angle left between projecting portions of the cerebellar and pyramidal tracts, and the tail stretching away ventrally along the outer margin of the lateral column outside the antero-lateral descending tract, the end of the tail often reaching to the ventral roots. It may be traced along the whole length of the cord, but is not so distinct and compact a tract as the two ascending tracts just mentioned; the fibres with ascending degeneration, that is to say, the fibres degenerating above the section or seat of injury, are very largely mixed with fibres of a different nature and origin. The medulla appears in the fibres of this tract at a relatively late period, during the eighth month.

We may further remark that these several tracts differ from each other, in some cases markedly, as to the diameter of their constituent fibres. Thus the cerebellar tract is composed almost exclusively of remarkably coarse fibres. The median posterior tract, on the contrary, is made up of fine fibres of very equable size, while the fibres of the antero-lateral ascending tract are of a size intermediate between the other two. The pyramidal tract on the other hand is made up of fibres of almost all sizes mixed together.

The tracts then which are thus marked out are, as descending tracts, the crossed and the direct pyramidal tracts, with the less distinct or important antero-lateral descending tract: and, as ascending tracts, the cerebellar tract the median posterior tract and the less distinct antero-lateral ascending tract. If we suppose all these tracts taken away there is still left a considerable area of white matter, namely, nearly the whole of the external posterior column, the external anterior column, including the region traversed by the bundles of the ventral roots, and that part of the lateral column which lies between the antero-lateral descending tract and the crossed pyramidal tract on the outside and the grey matter on the inside. From this area of white matter we may put on one side at present the external posterior column because, as we shall see, this column especially in its lateral part is largely composed of fibres of the dorsal root which leave it almost at once to pass to the grey matter; hence the alternative name of posterior root-zone. We may similarly leave for the present the small zone of white matter composed of very fine fibres known as *the marginal zone* or Lissauer's zone (Fig. 101, *L.*), lying dorsal and lateral to the tip of the dorsal horn and in the lower regions reaching to the outside of the cord; for this too belongs to the fibres of the dorsal root. If we take these parts away there remains an area of white matter immediately surrounding the grey matter on its lateral and ventral aspects. This area is characterised by the feature that no tracts of either descending or ascending degeneration can be traced in it after section of or injury to the cord. This feature is due to the fact that the area is composed of fibres which starting from cells within the cord run for a very short distance only in the white matter and soon end in connection with some other cells also within the cord. Such fibres do degenerate, like other fibres, when cut away from their trophic cells, but since they run a very short course their degeneration can be traced for a short distance only from the section or injury causing their degeneration. If we examine sections of a spinal cord *immediately* above or below the level at which the cord has been cut across or injured (Fig. 103) we find a considerable number of degenerated fibres more or less scattered over the area in question; these are fibres, ascending or descending, which the section or injury has separated from their trophic cells. As in our examination we passed upwards or downwards from the level of the section or injury we should find that these degenerated fibres rapidly diminished in number and finally disappeared. The absence of degeneration in the area in question at a distance from the level of a section or injury is not due as was once thought to the fibres of the area not degenerating when cut away from their trophic centres or to their possessing second or vicarious trophic centres, but simply to their running for a short distance only in the area. The area is composed of fibres providing short intraspinal paths from the grey matter of one part to some grey matter not far off, and hence contrasting strongly with the fibres forming the tracts of descending and ascending degeneration spoken of above, which pass to or from the cord from or to structures outside the cord itself and run long distances. The fibres composing the area acquire their medulla before any of the tracts mentioned above. It may be added that some of the fibres

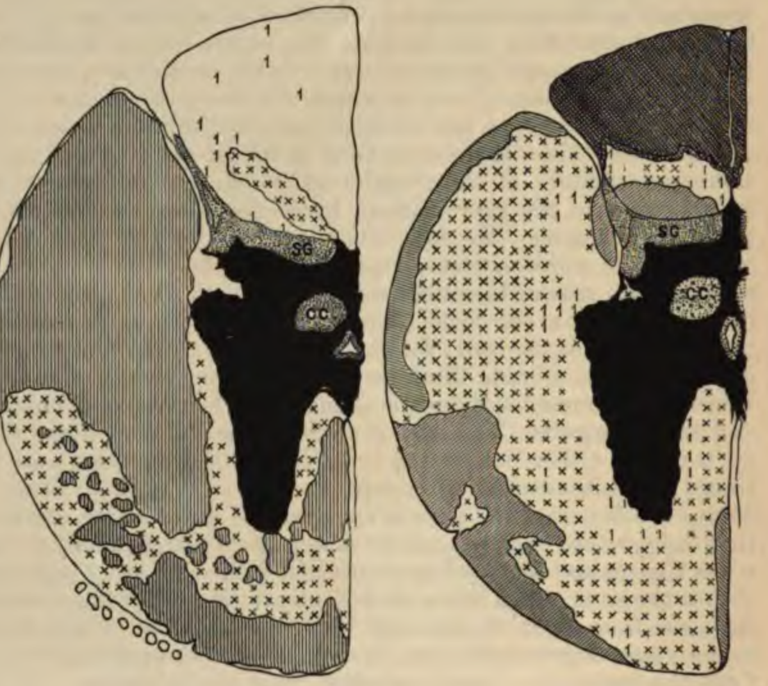


FIG. 103.

A, BELOW TRANSECTION. B, ABOVE TRANSECTION.

FIG. 103. CHARTS OF CROSS-SECTIONS OF THE SPINAL CORD (MONKEY) showing the topography of the degeneration consequent on a transection carried out at the 10th thoracic level. A, one segment below the transection; B, one segment above.

Cross-hatching means "absolute" degeneration, *i.e.* less than 1°/$_0$ fibres remaining sound. Simple hatching /// means "severe" degeneration. ×× means "slight" degeneration. Numerals 1, 2, indicate the places of scattered single or double fibres observed to be in degeneration. The spongy grey matter is shown as a black field, the gelatinous grey and Clarke's column (*CC.*) are stippled.

In A, the degenerations being below the injury are called *descending*.

In B, the degenerations being above are *ascending;* note that the latter involve *CC.* as well as the white matter.

forming the descending comma tract are like those of the area in question, short, intraspinal fibres.

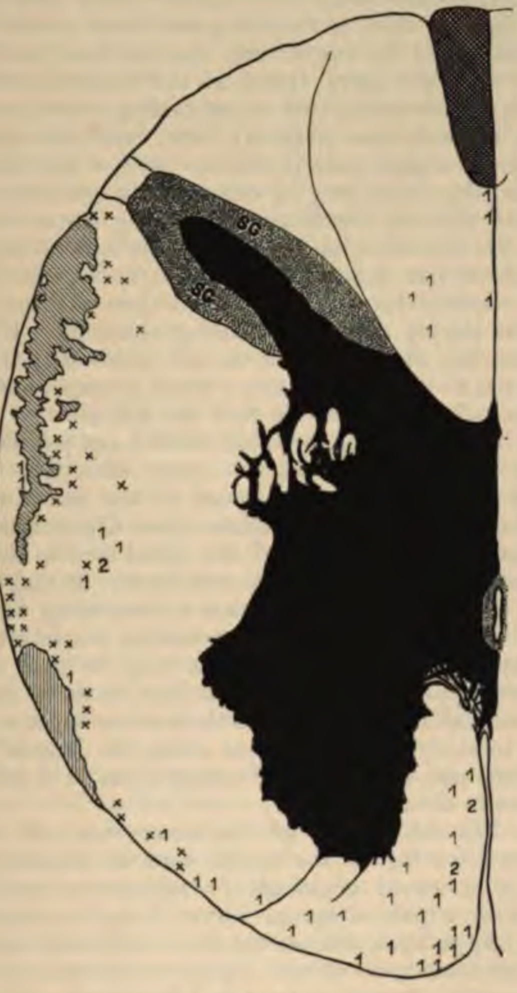


FIG. 103 C.

From the same experiment as the preceding and drawn to the same scale but at the 2nd cervical level. The same signs are used for denoting the degeneration. The patch of degeneration in the dorsal column is still "absolute" in character, but its area measures less than half that in B. The long tract of "severe" degeneration in the dorsal part of the lateral column is the direct cerebellar tract, which in monkey is partly shut off from the free edge of the column by fibres of the pyramidal tract. In man this is not so. Vide Fig. 101.

Compare these three charts with the diagrams given of the spinal tracts in Fig. 107.

§ **568**. It may be as well perhaps to insist here once more, that when these several tracts or the fibres running in the tracts are spoken of as ascending or descending, what is meant is that the degeneration takes place above the section or seat of injury or disease in the one case, and takes place below in the other. It has been supposed by many that the nervous impulses which these fibres severally carry, travel in the same direction as that taken by the degeneration, that the ascending tracts carry impulses from below upward, that is to say, carry impulses which arising from peripheral organs pass to various parts of the spinal cord or of the brain, that they are, in other words, channels of afferent impulses, and that conversely the descending tracts carry efferent impulses. To this view is often added as a corollary, that the tracts which do not degenerate at all carry impulses both ways, and hence cannot be considered as either afferent or efferent channels but simply as communicating channels. Upon this it may be remarked that impulses do not necessarily travel in the same direction as the degeneration; when a spinal nerve trunk is divided the afferent fibres as well as the efferent fibres both degenerate in a descending direction towards the periphery, though the former carry impulses in the other direction. Hence the direction of degeneration is no proof of the direction in which impulses travel; moreover, as we have seen, degeneration does not actually travel along the fibres of the spinal cord in the same way that it does along the fibres of a nerve trunk. It may be that the descending tracts do carry impulses in a descending direction, that is, efferent impulses, and that the ascending tracts serve to carry afferent impulses; but the proof that they do thus respectively act must be supplied from other facts than those of degeneration. Moreover, we shall have to return to these ascending and descending tracts and to study their behaviour along the length of the cord before we can use the facts concerning them as a basis for any discussion as to their functions.

§ **569**. *The connections of the nerve-roots.* If following a common view we regard the spinal cord as resulting from the fusion of a series of segments or metameres, each segment, represented by a pair of spinal nerves, being a ganglionic mass, that is to say a mass containing nerve-cells with which nerve-fibres are connected, we should expect to find that the fibres of a spinal nerve soon after entering in, or before issuing from the spinal cord are connected with nerve-cells lying in the neighbourhood of the attachment of the nerve to the cord. And this to a certain extent is actually the case, more especially in respect to the issuing nerve-fibres; but as regards the entering nerve-fibres such an arrangement is obscured by other developments.

With regard to the *ventral root*, there can be no doubt that a very large proportion of the fibres in the root are continuations of the axis-cylinders or axons of the large cells in the ventral horn of the same side. The fibres which can thus be traced are of large diameter, and appear to be chiefly if not exclusively motor fibres for the skeletal muscles. But the ventral root contains other than motor fibres for the skeletal muscles, vaso-motor fibres for instance, secretory fibres and others; and these probably have a different origin. And indeed some of the fibres of the root arise not from large but from small cells in the ventral horn, while others have been traced through the ventral horn, on the one hand towards the dorsal horn and on the other hand towards the lateral column; others again are found to pass through the ventral horn of their own side to the bottom of the ventral fissure where, crossing over to the other side and thus forming part of the white commissure, they appear to proceed to the ventral horn of the other side. We cannot at present make any positive statement as to the real origin and exact nature of these fibres which thus upon entering the cord pass by the cells in the ventral horn without joining them, though those which cross by the white commissure are supposed to take origin in the cells of the ventral horn of the other side; it is sufficient for our present purposes to remember that while a large number of the fibres of the ventral root, presumably those supplying the skeletal muscles, take origin in the cells of the ventral horn, shortly before they issue from the cord, others have some other origin. And similarly we have reason to think that all the cells in the ventral horn do not send out axis-cylinder processes to join the ventral roots of the same side. We may however regard a large number at all events of the cells of the ventral horn, at the level of as well as a little below and a little above the level of the exit of any particular ventral root, as constituting a sort of nucleus of origin for the larger number of the fibres, and those most probably the skeletal motor fibres, of that ventral root.

The *dorsal root* enters the cord not in several bundles laterally scattered as does the ventral root, but in a more compact mass. This mass however consists of at least two distinct bundles, which upon their entrance into the cord take different courses. One bundle, the larger one, lying to the inner or median side of the other, consisting of relatively coarse fibres, and called the *median bundle* (Fig. 99, *P.r'*), passes obliquely into the lateral part of the external posterior column, which, as we have said, is in consequence often spoken of as the posterior root-zone. The other smaller bundle placed to the outside of the former, and called the *lateral bundle* (Fig. 99, *P.r*), may be again divided into an *intermediate bundle* (Fig. 100, *Pr*) lying next to the median bundle, and into a still more lateral bundle (Fig. 100, *Pr''*). The former, consisting also of coarse fibres, plunges directly through the substance of Rolando at the extremity of, and so into the grey matter of the horn, where the fibres in part at least changing their direction run longitudinally in the grey matter in bundles known as "the longitudinal bundles of the dorsal horn," Figs. 99, 100 *r. f. p.* The small most external or lateral portion of the lateral bundle, consisting of fine fibres and sometimes spoken of as *the* lateral bundle, on entering the cord at once take a longitudinal direction, and thus forms the thin layer of fine fibres, the posterior marginal zone or Lissauer's zone, indicated in Fig. 100 by *m. t.*, which lies between the actual extremity of the horn and the surface of the cord, and in the upper regions of the cord (cf. Fig. 99, *p'*), runs some way upward on the lateral margin of the horn between the grey matter and the crossed pyramidal tract.

Thus much may be learnt by the ordinary methods of preparation. The degeneration method further teaches us, as we shall presently see, that many of the fibres of the median bundle after running for a certain distance in the lateral part of the posterior column pass into the median part and go to form the median posterior tract; some of these fibres from each root, as we shall also see, may be traced in this tract along the whole length of the cord until they end in the bulb, some few passing still higher up.

The special silver and methylene-blue methods mentioned above (§ 564) have also taught us the following:

A fibre of the dorsal root (and so far as we can judge each of its fibres) on entering the cord divides into two, one division running forward towards the head, the other backward towards the hind end, the former however having the longer course. Each fibre thus arising by division gives off along its course collaterals, the terminations of the collaterals and of the fibre itself being in the form of arborescences attached to the body of the processes of some or other cells. Some of the fibres thus end in connection with the cells of Clarke's column (vesicular cylinder) of the same side, others in connection with cells in the substantia gelatinosa also of the same side. Of those fibres which run in the median posterior tract a large number end in connection with certain cells in the spinal bulb. And the endings in connection with these three sets of cells, those of Clarke's column, of the substantia gelatinosa, and of the spinal bulb, all of the same side, may be regarded as the main endings of the fibres of the dorsal root. But we have reason to think that some of the fibres make connections with the (motor) cells of the ventral horn of the same side (and so provide a direct mechanism for certain simple reflex movements), while others end in connection with cells lying in the grey matter of the other side of the cord. But we shall have to return to these matters later on in their appropriate place.

§ **570**. *The Special Features of the several regions of the Spinal Cord* (in Man). The cord begins below in the slender filament called the *filum terminale*, which lying in the vertebral canal, in the midst of the mass of nerve-roots called the *cauda equina*, rapidly enlarges at about the level of the first lumbar vertebra into the *conus medullaris*. This may be regarded as the beginning of the lower portion of a fusiform enlargement of the cord known as the *lumbar swelling*, which reaches as high as about the attachment of the roots of the twelfth or eleventh thoracic nerve at the level of the eighth thoracic vertebra, the broadest part of the swelling being about opposite the third lumbar nerve. Above the lumbar swelling, through the thoracic region the somewhat narrowed cord retains about the same diameter until it reaches the level of the first or second thoracic nerve opposite the seventh cervical vertebra where a second fusiform enlargement, the *cervical swelling*, broader and longer than the lumbar swelling, begins. The broadest part of the cervical swelling is about opposite to the fifth or sixth cervical nerve; from thence the diameter of the cord becomes gradually somewhat less until it begins to expand into the bulb, but even in the highest part is greater than in the thoracic region. The sectional area of the cord increases therefore from below upwards, but not regularly, the irregularity being due to the lumbar and cervical swellings.

The extremity of the filum terminale is said to consist entirely of neuroglia closely invested by the membranes, even the central canal being absent. A little higher up the central canal begins, and nerve-cells with nerve-fibres make their appearance in the neuroglia; thus a kind of grey matter covered by a thin superficial layer of white matter is established. We have already referred to the peculiar features of the lower end of the conus, § 565; but higher up the canal becomes central and small, the posterior columns are developed, and the grey matter contains more nervous elements and relatively less neuroglia, becoming in fact ordinary grey matter. From thence onward to very near the junction with the bulb, where transitional features begin to come in, the spinal cord may be said to have the general structure previously described.

The sectional area of the white matter increases in absolute size and on the whole in a steady manner from below upwards. In other words, in a section at any level, the number of longitudinal fibres forming the white matter is greater than the number at a lower level, and less than the number at a higher level; for any difference which may exist in the diameter of the individual fibres is insufficient to explain the differences in the total sectional area of the white matter. If we were to measure in man the sectional area of each of the spinal nerves as it joins the cord, and to add them together, passing along the cord from below upwards, the results put in the form of a curve would give us some such figure as that shewn in Fig. 104; the area gained by adding together the sectional areas of the nerves increases in a fairly steady manner from below upwards. The curve of the sectional area of the white matter of the cord taken from below upwards would be very similar, but if anything more regular. It must be understood however that the dimensions of the areas would not be the same in the two cases. The sectional area of the white matter at the top of the cervical region, though greater than anywhere lower down, is far less than the united sectional area of all the nerves below that level. The white matter is not formed by all the fibres from the nerves which join the spinal cord continuing to run along the cord up to the brain; as we have seen, some at least of the fibres end in the grey matter. Nevertheless the white matter in passing up the cord appears to receive a permanent addition at the entrance of each nerve. We may infer that each nerve has a representative of itself starting from the level of its entrance and running up to some part of the brain. Whether the fibres thus representative of the nerve are continuations of the very fibres of the nerve itself, or are new fibres starting from some relay of grey matter, with which the fibres of the nerve are also connected, is another question.

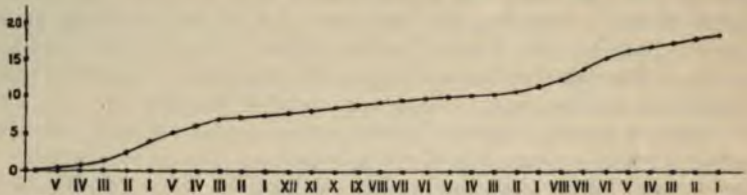


Fig. 104. Diagram shewing the united sectional areas of the Spinal Nerves, proceeding from below upwards.

In this as in the succeeding figures 102—3, —5, —6, —7, all of which refer to man, the left-hand side represents the bottom of the cord and the right-hand the top of the cord, the numerals indicating successively the sacral, lumbar, thoracic and cervical nerves. The several figures are not drawn to the same scale.

§ **571.** The grey matter in contrast to the white matter shews great variations in area along the length of the cord (Fig. 105). From the entrance of the coccygeal nerve upwards the area increases very rapidly, reaching a maximum at about the level of the 5th lumbar nerve. It then rapidly decreases to about the level of the 11th thoracic nerve, maintains about the same dimensions all through the thoracic region, and begins to increase again at about

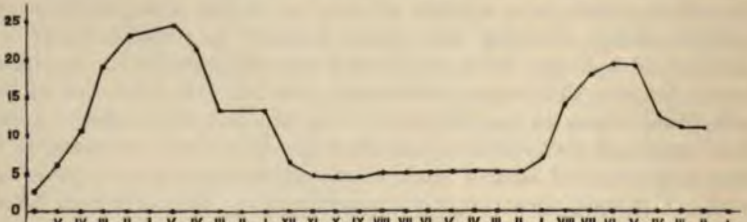


Fig. 105. Diagram shewing the variations in the sectional area of the grey matter of the Spinal Cord, along its length.

the level of the 2nd thoracic nerve. Its second maximum is reached at about the level of the 5th or 6th cervical nerve, after which the area again becomes smaller, remaining however at the upper cervical region much larger than in the thoracic region.

The meaning of these variations becomes clear when we turn to Fig. 106, which shews in a similar diagrammatic manner the sectional areas of the several spinal nerves. It will be observed that the increase and decrease of the sectional area of the grey matter follow very closely the increase and decrease of the quantity of nerve, that is to say, neglecting differences in the diameter of the fibres, in the number of nerve-fibres passing into the cord. The sectional areas of the 1st and 2nd sacral, 4th and 5th lumbar nerves are very large, and opposite to these the sectional area of the grey matter of the cord is very large also; the enlargement of grey matter which is the essential cause of the lumbar swelling is correlated to the large number of fibres which enter and leave the cord at this region to supply chiefly the lower limbs. Similarly the enlargement of grey matter which is the essential cause of the cervical swelling is correlated to the large number of fibres which enter and leave this region of the cord to supply chiefly the upper limbs. In the thoracic region, where the number of fibres entering and leaving the cord is relatively less, the sectional area of the grey matter is also less. Since the attachments of the several spinal nerves are not exactly equidistant from each other along the length of the cord, the sectional area is not an exact measure of bulk; the total bulk of grey matter for instance belonging to two nerves which enter the cord close together is less than that of two nerves giving rise to the same sectional area of grey matter as the former two but entering the cord far apart from each other. Still the error which may be introduced by taking sectional area to mean bulk is, for present purposes at all events, so small that we may permit ourselves to say that in the successive regions of the spinal cord the bulk of grey matter in any segment is greater or less according to the size of the nerve (or pair of nerves, right and left) belonging to that segment.

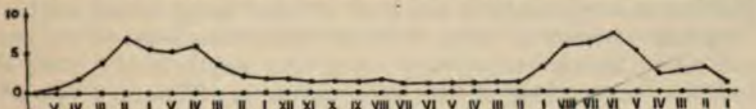


FIG. 106. DIAGRAM SHEWING THE RELATIVE SECTIONAL AREAS OF THE SPINAL NERVES, AS THEY JOIN THE SPINAL CORD.

From this anatomical fact we appear justified in drawing the conclusion that at all events a great deal of the grey matter of the spinal cord may be considered as furnishing a nervous mechanism, with which the efferent fibres of each spinal nerve just before they leave the cord, and the afferent fibres soon after they join the cord, are more immediately connected. This need not mean that the whole of the grey matter is thus directly connected with and thus rises and falls with the fibres of the nerves; it might mean that there is a sort of core of grey matter, which maintains a uniform bulk along the whole length of the cord and serves as a basis which is here more and there less swollen by the addition of the grey matter more immediately connected with the fibres of the nerves. This question the method which we are now using cannot settle.

§ **572**. Owing to these different rates of increase of the grey and white matter respectively along the length of the cord, we find that in sections of the cord taken at different levels the appearances presented vary in a very distinct manner. This is strikingly shewn by comparing Figs. 96, 99 and 100. At the level of the third lumbar nerve (Fig. 100) the grey matter is very large, reaching, as we have seen, its maximal sectional area at about this point, so that although the area of white matter is not very great the whole area of the cord is considerable.

At the level of the sixth thoracic nerve (Fig. 96), in spite of the white matter having very decidedly increased, the grey matter has shrunk to such very small dimensions, that the total sectional area of the cord has markedly diminished.

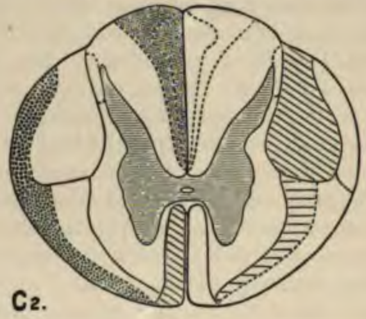
At the level of the sixth cervical (Fig. 99) the grey matter has again increased, reaching here as we have seen its second maximum; the white matter has also further increased, and that indeed very considerably, so that the total area of the cord is much greater than in any of the lower regions.

Further details of the varying size of the white matter and of the grey matter at different levels are also shewn in the series given in Fig. 107. In these, combined with the three figures just referred to, it will be observed that the serial increase and decrease of the grey matter does not affect all parts of the grey matter alike, so that the outline of the grey matter changes very markedly in passing from below upwards. In the coccygeal region each lateral half is a somewhat irregular oval, and in the sacral region, Fig. 107, *Sac*, the differentiation into ventral and dorsal horns is still very indistinct. In the lumbar region the two horns are sharply marked out, though both the dorsal and ventral horns are broad and more or less quadrate. In the thoracic region the decrease of grey matter has affected both horns, so that both are pointed and slender, while the junction between them has not undergone so much diminution, so that what has been called the lateral horn is relatively conspicuous. In the cervical region the returning increase bears much more on the ventral horn which again becomes large and broad, than on the dorsal horn which still remains slender and pointed. Taking the form of the grey matter in the thoracic region as the more typical form of the grey matter we may say that while the increase on the lumbar swelling bears equally on the ventral and dorsal horns, that in the cervical region bears chiefly on the ventral horn.

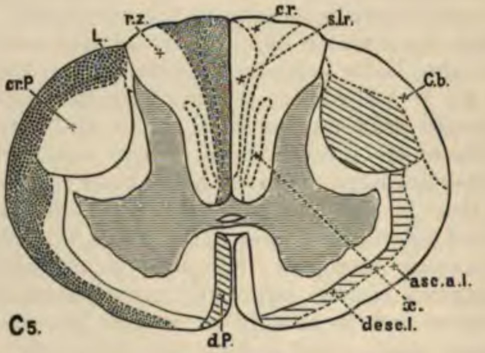
Now we have no reason to suppose that either centripetal impulses reach the lumbar spinal cord in greater numbers from the lower limbs, or along any of the nerves joining this part of the cord, or that those which do reach it are of a more complex nature than is the case with the centripetal impulses reaching the cervical cord along the nerves of the upper limbs. The increase of grey matter in the dorsal horns is therefore not correlated to any increase in the number or complexity of the centripetal impulses reaching the cord; and we may, provisionally, conclude that at least a large part of the grey matter in the dorsal horn is not specially concerned in any elaboration or transformation of centripetal impulses immediately upon their arrival at the cord. Indeed we have seen that while there is ample evidence to connect the nerve-cells, and therefore presumably the grey matter in general of the ventral horn with the centrifugal motor fibres of the ventral root, there is no corresponding evidence as to any large immediate connection of the centripetal fibres of the dorsal root with the nerve-cells or indeed any other part of the grey matter of the dorsal horn. We may add that, as we shall point out later on, so essential is the concurrence of appropriate centripetal impulses to the due carrying-out of complex coordinate motor or centrifugal impulses, that we can scarcely expect to find any increase in the nervous mechanisms devoted to the purely motor function of carrying out motor impulses without a corresponding increase in the nervous mechanisms belonging to the centripetal impulses, by means of which those motor impulses are guided and coordinated. Hence, were the latter nervous mechanisms restricted to the dorsal horns we should expect to find a greater parallelism than does actually exist between them and the ventral horns.

§ **573**. The changes in the area of grey matter illustrated by the statements and diagrams given above refer to the grey matter as a whole, that is, not only to nerve-cells, but also to strands and networks of nerve fibres and nerve fibrils, and indeed include to a certain extent neuroglia. We have seen § 566 that we are able to distinguish certain large and conspicuous nerve-cells in the grey matter and to arrange these into groups. The grey matter contains many other small nerve-cells, which we are not able at present to name or arrange, but whose existence must always be borne in mind. Confining ourselves now however to the groups of larger, more conspicuous nerve-cells, we find that, broadly speaking, the chief differences which can be observed in the cells of the ventral horn along the length of the cord are that in the thoracic region the nerve-cells of the ventral horn are few, and relatively small, while in the cervical and lumbar region, especially in the latter, they are numerous and large. It is not easy, even if possible, to distinguish in the thoracic region the several groups of cells marked in Figs. 99, 100 as **2**α, β, γ: the median group (Figs. 99, 100, **1**), indeed seems to be the only group present in the mid-thoracic region (Fig. 96, **1**). The group of the dorsal horn (Figs. 96, 99, 100, **6**) appears to be about the same in all regions.

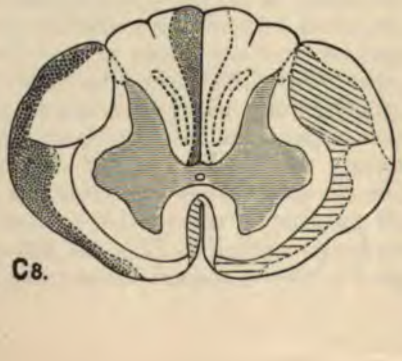
With two other groups of nerve-cells striking differences are seen in different regions. The vesicular cylinder, for instance (Fig. 96, **3**), is most conspicuous in the thoracic region. It may be said to reach from about the 8th cervical nerve to the 3rd lumbar nerve, being perhaps most developed in the lower thoracic and upper lumbar region. It is absent in the cervical region above the 7th or 8th cervical nerve, and in the lumbar region below the 3rd lumbar nerve; but a similar group of cells is



C2.



C5.



C8.

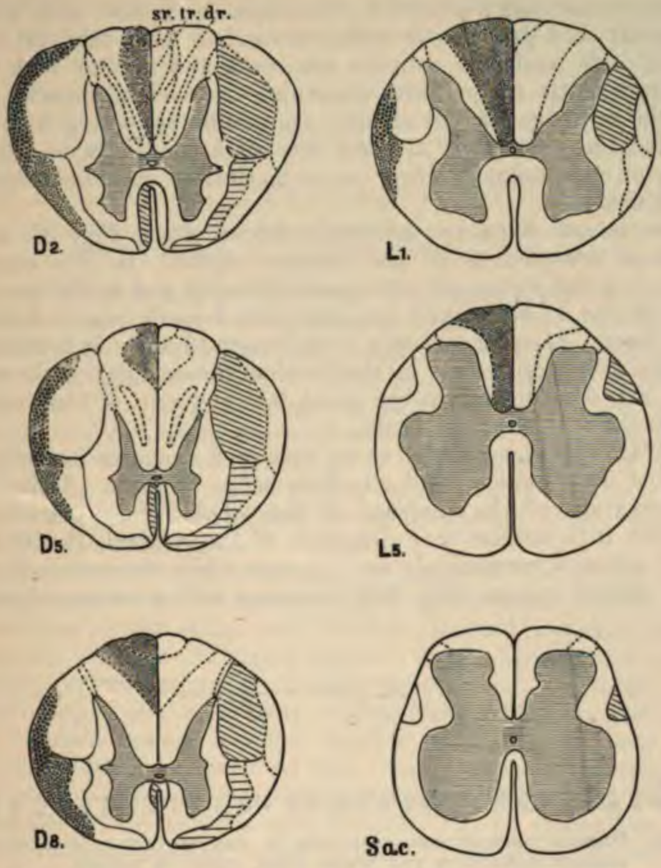


FIG. 107. DIAGRAM ILLUSTRATING SOME OF THE FEATURES OF THE SPINAL CORD AT DIFFERENT LEVELS. (Sherrington.)

All the figures are drawn to scale, and represent the cord magnified four times. They shew the differences at different levels in the shape and size of the cord, in the outline of the grey matter, and in the relative position of the anterior and posterior fissures, and also shew the variations at different levels of the several 'tracts' of the white matter.

C_2 at the level of the second cervical nerve, C_5 of the fifth cervical, C_8 of the eighth cervical. D_2 of the second thoracic, D_5 of the fifth thoracic, L_1 of the first lumbar, L_5 of the fifth lumbar, and Sac. of the second sacral nerve.

The shading of the tracts is a little different from that in Fig. 101. In the median posterior column of D_2 the areas of fibres coming from the sacral nerves *s.r.* and lumbar nerves *l. r.* are distinguished from the area, *d. r.*, of fibres belonging to the thoracic nerves. In C_8, no distinction is made between any of these sets of fibres; in L_5 only fibres of sacral nerves are represented; in L_1 D_8 D_5, the more dorsal small portion corresponds to sacral fibres and the next to lumbar, or lumbar thoracic nerves.

present opposite the 2nd and 3rd cervical nerves; a group of more doubtful likeness is seen in the sacral region below; and the column is said to have a representative in the bulb above the spinal cord proper. It seems natural to infer that the cells forming this vesicular cylinder are connected neither with the ordinary somatic motor fibres governing the skeletal muscles, nor with the ordinary afferent sensory, somatic fibres coming from the skin and elsewhere, but in some way with some special sets of fibres; on this point however no authoritative statement can as yet be made.

The lateral horn or intermedio-lateral tract, Fig. 96, **4**, is also most conspicuous in the thoracic region. In the lumbar region it is lost or traced with great difficulty, and in the cervical region seems to be merged into the most dorsally placed division of the lateral group of the cells of the ventral horn. It is possible that this group represents in the limbless thoracic region the cells which are developed into the great lateral group of the ventral horn in the regions of the limbs.

§ 574. The white matter as we have seen increases in sectional area with considerable regularity from below upwards. If instead of a diagram of the increase of the whole white matter, we construct in a similar way diagrams of the ventral, dorsal and lateral columns respectively we find that while the sectional area of the lateral column (Fig. 108) increases with some considerable regularity from below upwards, though not so regularly as does the whole area of white matter, both the ventral (Fig. 109) and the dorsal (Fig. 110) columns agree to a certain extent with the grey matter in shewing a decided increase in both the lumbar and the cervical swellings. We may, provisionally at least, infer from this that, while considerable portions of both the ventral and

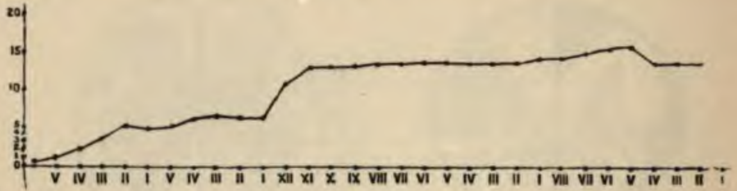


Fig. 108. Diagram shewing the variations in the sectional area of the lateral columns of the Spinal Cord, along its length.

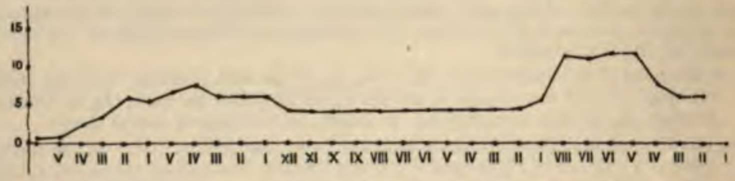


Fig. 109. Diagram shewing the variations in the sectional area of the anterior columns of the Spinal Cord, along its length.

the dorsal columns are like the adjoining grey matter in some way or other concerned in the exit and entrance of efferent and afferent fibres, the larger portion of the lateral column is concerned in the transmission of impulses to and fro, between the local mechanisms below, immediately connected with the several spinal nerves, and the brain above. This conclusion seems incidentally confirmed (though these diagrams must not be strained to carry detailed inferences) by the sudden increase of the lateral column above the lumbar swelling, as if the large mass of nervous mechanism for the lower limbs concentrated in this region demanded a sudden increase in the number of fibres connecting it with the brain above.

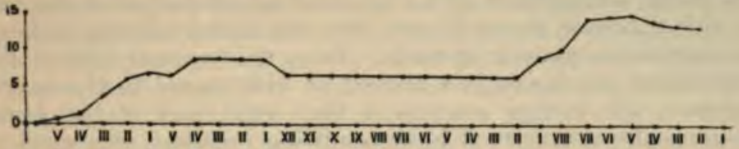


FIG. 110. DIAGRAM SHEWING THE VARIATIONS IN THE SECTIONAL AREA OF THE POSTERIOR COLUMNS OF THE SPINAL CORD, ALONG ITS LENGTH.

This more or less continuous increase of the lateral column partly explains the change of form in the general outline of the transverse section of the cord which is observed in passing upwards from the lower to the higher regions. In the coccygeal, sacral and lumbar regions the outline, though varying somewhat chiefly owing to the disposition of the grey matter, is on the whole circular. As the thoracic passes into the cervical region, the increase of the lateral columns increases the side to side diameter so much that the section becomes oval, and in the cervical swelling itself this increase of the side to side diameter out of proportion to the dorso-ventral diameter is very marked. The actual outline of the whole transverse section is however determined also to a certain extent by the changes of form of the grey matter.

The cord moreover undergoes along its length a change which is not very clearly indicated in the diagrams Figs. 108, 110. By comparing the series of transverse sections given in Fig. 107 it will be seen that the relative position of the central canal shifts along the length of the cord. In the sacral and lumbar regions the central canal is nearly at the centre of the circle of outline, and the dorsal and ventral fissures are nearly of equal depth. Even in the upper lumbar region, and still more in the thoracic region, the position of the central canal is shifted nearer to the ventral surface, so that the dorsal fissure becomes relatively longer, deeper, than the ventral. This shifting goes on through the cervical region up to about the level of the 2nd cervical nerve, where it is arrested by the beginning of the changes through which the spinal cord is transformed into the far more complicated bulb.

This lengthening of the dorsal fissure indicates an increase in the dorso-ventral diameter of the dorsal columns, and this, not being accompanied by a compensating diminution of the side to side diameter, shews in turn that the dorsal columns undergo an increase in passing upwards. From this we may add to the provisional conclusion just arrived at with regard to the lateral columns, the further conclusion that some part of the dorsal columns also is concerned in transmitting impulses, in a more or less direct manner, between the various regions of the cord below and the brain above. The ventral columns do not increase in the same marked manner, though over and above the increase due to the lumbar and cervical swellings, a continued increase may be observed, especially in the upper cervical region; it is in this upper region that the direct pyramidal tract is best developed.

§ **575.** The provisional conclusions at which we have arrived are further, to a certain extent at least, confirmed and extended by a study of the behaviour at the several regions of the cord of the special tracts of white matter described in § 567.

The pyramidal tract, that is to say, the crossed pyramidal tract entering the spinal cord above from the pyramid is very large in the cervical region, having the form and situation shewn in Fig. 107, $C_2C_5C_8$. From thence downward it diminishes in size, the diminution being especially rapid in the lumbar swelling, Fig. 107, L_1, where the tract being no longer covered in by the cerebellar tract comes to the surface of the cord; but it may be traced by the degeneration method down as far as the coccygeal region, and indeed appears to be coexistent with the issue of spinal nerves from the cord. Diminution of the tract means a lessening of the number of fibres; and since we cannot suppose that any of the fibres come suddenly to an end in the tract itself we are led to infer that along the cord, from above downwards, fibres are successively leaving the tract and passing to some other part of the cord. We seem further justified in concluding that the fibres which thus successively leave the tract go to join the series of local nervous mechanisms with which the spinal nerves communicate, as we have seen reason to believe, upon their entrance into the cord. Indeed, as we shall see later on, we have reason to think that the nervous mechanisms which the fibres in question join are those belonging to the motor fibres of the ventral roots; the fibres of the pyramidal end by forming synapses with the cells whose axons go to form the fibres of the ventral roots. This pyramidal tract does not begin in the pyramid, but may be traced through the lower parts of the brain right up to special areas in the cortex or surface of the cerebral hemispheres; and very strong reasons may be brought forward in support of the view that the fibres of this tract are fibres which carry impulses from the cortex to successive portions of the spinal cord, and there give rise to efferent impulses which pass to appropriate skeletal muscles. The tract, therefore, is not only a descending tract by virtue of the mode of degeneration, but may be spoken of in a broad sense as a tract of efferent impulses descending from the cerebral cortex; and indeed it is maintained that it is the channel of the particular kind of efferent impulses which we shall speak of as voluntary or volitional impulses. We may add that as the tract passes along a path which we shall subsequently describe, from the cerebral cortex through the lower parts of the brain to the pyramid, it gives off fibres to mechanisms connected with several of the cranial nerves, much in the same way that it gives off fibres to those connected with the spinal nerves.

We may therefore picture to ourselves this pyramidal tract as starting in the form of a broad sheaf of fibres from a certain district on the surface of one of the cerebral hemispheres. Putting aside for the present any possible increase of the number of fibres by division (though we have reason to think that this does to a certain extent occur) we may regard the tract as being at its maximum at its beginning in the cortex. As it descends to the decussation of the pyramids in the bulb it loses a certain number of fibres, which pass off to the cranial nerves. Having crossed and entered into the lateral column of the cord it continues to give off fibres which make connections with the nerve-cells giving rise to the ventral roots of the spinal nerves, probably of each in succession, and so goes on its way down the cord continually diminishing until the last remaining fibres are given off to the last coccygeal nerve.

When degeneration is set up along this tract, as may be done, by injuries to particular areas of the cerebral cortex, the main mass of degenerated fibres, after crossing over from one side of the cerebrospinal axis to the other in the decussation of the pyramids at the lower end of the bulb, during its further progress down the spinal cord, keeps to the side to which it has crossed right down to the end. Hence, as we have said, it is called the crossed pyramidal tract. The main mass of fibres, the degeneration of which has been started by injury to the left side of the brain, crosses over to the right side of the spinal cord and runs down the lateral column of the right side to the end of the cord. Nevertheless some of the fibres of the pyramid pass directly to the lateral column of the same side, forming the area of scattered fibres shewn in Fig. 107 *P′*.

The direct pyramidal tract (Fig. 107, *dP*), except that it does not cross at the decussation of the pyramids, is otherwise similar to the crossed pyramidal tract, and indeed is a part of the same strand to which the crossed tract belongs. When degeneration in this tract is started by injury to particular areas of the cerebral cortex, say on the left half of the brain, the degeneration may be traced through the left ventral pyramid, and so to the left median ventral column of the spinal cord. The direct tract is never so extensive or marked as the crossed tract, does not reach so far down, is much more variable both in length and in sectional area and, as we have said, is almost confined to man. Diminishing as it descends it may be said to cease in the middle thoracic region, Fig. 107, D_5D_8. Taking an average we may say that, of the whole strand running in the pyramids above the decussation, about three-fourths of the fibres go to form the crossed and about one-fourth to form the direct tract. We shall see later on that the impulses coming down along the united tract in the brain may, broadly speaking, be said to cross over wholly from one side to the other before they reach the skeletal muscles, so that the impulses passing along fibres in, say, the left pyramid, reach the muscles of the right limbs and right side of the body whether the fibres cross over at the decussation to form the crossed or remain on the same side to form the direct pyramidal tract. We are therefore led to infer that the fibres in the direct tract, as they pass down the cord, cross over in the cord itself before they make connections with the cells belonging to the ventral roots. Probably the crossing is effected by means of some of the decussating fibres which form the ventral white commissure. A part only, indeed a small part, of the commissure can serve this purpose; most of the fibres of the commissure, and in the lower regions of the cord, where the direct tract no longer exists, all the fibres must have some other functions. Some of the fibres of this great pyramidal tract, leave the tract, as we have said, to join some of the cranial nerves before the pyramids of the bulb are reached; and the impulses passing along these fibres also cross over to the opposite side before they issue along the cranial nerves. Hence we infer that these fibres decussate above the decussation of the pyramids just as those of the direct tract decussate below it. So that of the whole strand as it leaves the cerebral cortex, while the main mass of fibres crosses over at the decussation of the pyramids, the rest of the fibres cross the middle line in succession from the level of the third cranial nerve to the level of the lower limit of the direct tract; below the decussation of the pyramids the crossing takes place by means of the ventral commissure of the cord, above the decussation by means of what we shall later on learn to speak of as the raphe of the bulb, or by structures corresponding to this higher up.

§ **576**. The *cerebellar tract* (Fig. 107, *Cb*) is as we have seen a tract of ascending degeneration; the degeneration in it makes its appearance above the section or the seat of other injury of the cord. It begins somewhat suddenly at the level of the second lumbar nerve, being absent at least as a distinct tract below; injury of the cord at the level of the middle and lower lumbar nerves leads to no marked tract of degeneration (though possibly scattered single fibres may degenerate), while injury higher up does. The tract lies, as we have said, close to the surface of the cord in the dorsal part of the lateral column just outside the crossed pyramidal tract, and while varying somewhat in the shape of its section from level to level remains throughout a somewhat narrow crescentic patch. At the top of the spinal cord it passes, as we have said, from the lateral columns into the restiform bodies of the bulb, and so to certain parts of the cerebellum.

When the section or lesion is limited to one side of the cord, the degeneration is similarly limited to the same side, and that along its whole course up to the cerebellum; there is no evidence of any of the fibres decussating in the cord.

The area of the tract increases from below upward. This has been determined by the embryological method, by noting the appearance of the medulla in the fibres, as well as by comparing the extent of the degeneration following upon a section high up in the cord with that following upon a section lower down. From this we infer that the fibres composing the tract must start successively from other parts of the cord along its length, that is to say, the tract must be fed by fibres coming from other structures in the cord. On the other hand, it is found that the degenerated area following upon a section or injury diminishes as it is traced upward; when, for instance, a section is made in the mid-thoracic region the area of degeneration in the tract is greater immediately above the section than it is higher up, say in the cervical region. From this we are led to infer that though the tract is successively fed along its course by fibres coming from other parts of the cord, some of the fibres entering the tract, though like their companions undergoing an ascending degeneration, do not like them continue in the tract right up to the cerebellum, but pass off to other parts of the cord on their way upward. This, however, is equivalent to saying that the tract is not a pure or homogeneous one, but consists of at least two sets of fibres, only one of which is continued on to the cerebellum and strictly deserves the name of 'cerebellar.' It may perhaps here be mentioned that while the fibres composing the tract are as a whole conspicuously coarse, large fibres, with these there are mingled, especially in the thoracic region, a number of much finer fibres; but these apparently undergo a descending not an ascending degeneration and do not therefore really belong to the tract; they may be fibres which have strayed from the pyramidal tract.

Unlike the case of the median posterior tract of which we have next to speak, no degeneration, at least in the lumbar and thoracic regions, appears in the cerebellar tract after section merely of the roots of the nerves; to produce the degeneration the cord itself must be injured. From this we may infer that the tract is not fed directly by the fibres of the posterior roots. And there is increasing evidence that the tract is fed by fibres coming from the vesicular cylinder, that these cells send out axons which passing laterally become the fibres of the tract. From the fact that the degeneration taking place in it is an ascending one, it is supposed that the tract is the channel for ascending, that is to say, in a broad sense, afferent impulses. And considerable interest attaches to the fact that these impulses should be carried, not to the cerebrum but to the cerebellum. Our knowledge on this point, however, is still imperfect, and what can be said in the matter had better be said later on.

§ **577.** The *median posterior* tract is the other conspicuous tract of ascending degeneration; it also is supposed to be a channel for ascending, afferent impulses; and this view is rendered almost certain by the intimate relations of the tract to the fibres of the posterior roots.

In dealing so far with the tracts of degeneration in the spinal cord we have always spoken of the degeneration as being the result of lesions of the spinal cord itself. Experiments on animals, however, and clinical experience have shewn that division or injury of the fibres of the dorsal roots is followed by tracts of degeneration in the spinal cord, though no damage whatever may have been done to the substance of the cord itself. These tracts make their appearance in the median posterior columns, the exact path and limits of the degeneration differing with the different spinal nerves. The results of the division of different groups of nerves are so instructive that we may dwell upon them in detail.

If the dorsal roots of two or three lumbar nerves (on one side) be divided, an examination of the cord, after an interval long enough to allow degeneration to be well established, will bring to light the following features. The divided roots will be found to have degenerated right up to their entrance into the cord. A section of the cord opposite the entrance of the lowest divided root will shew no degeneration of the cord beyond that of the bundles of fibres passing in. A little higher up degeneration will be observed in the external posterior column close to the dorsal horn; and as we ascend we find that this degeneration first spreads over a large portion of the external posterior column, and then invades the median posterior column; the degeneration does not affect the whole of the median posterior column but leaves intact a small dorsal portion, roughly triangular in shape, at the angle between the fissure and the dorsal surface of the cord, as well as some portion of the more ventral part of the column nearest the grey commissure. Still a little higher up we should find that degenerated fibres had disappeared from the external portion of the external posterior column close to the grey matter, though still existing in the more median part of that column, as well as in the median posterior column to the extent just indicated. Still a little higher up the whole of the degeneration would have disappeared from the external posterior column, but the tract of degeneration in the median posterior column would remain, the extent of degeneration being dependent on the number of roots which had been divided. Lastly, by carrying the sections still higher up the cord we should be able to trace this tract in the median posterior column right up to the bulb, where it would come to an end.

If we divided some of the thoracic nerves instead of the lumbar we should obtain very similar results: a degeneration of the external posterior columns a little above the entrance of the roots, spreading across the column towards the median line, and wholly disappearing at a certain height above, accompanied by a degeneration of a part of the median posterior column, reaching from a little distance above the entrance of the divided nerve-roots right up to the bulb. This latter tract of degeneration would however not occupy the same position as that consequent upon division of the lumbar nerves; its position would be more ventral, nearer the grey commissure, and rather more lateral. Compare Fig. 107, D_2, where *lr* indicates the degeneration due to section of the lumbar nerves, and *dr* that of the thoracic nerves. If we divided some of the cervical dorsal roots we should get similar results, with the difference that the tract of degeneration in the median posterior columns would occupy a position still more ventral and still more lateral (Fig. 107, C_5 *c.r.*); while if we divided the sacral nerves the tract of degeneration would be dorsal and median to the tract belonging to the lumbar nerves, and would occupy more or less of the triangle left below that tract (Fig. 107, D_2 *s.r.*). The degeneration it will be understood is in all cases confined to the same side of the cord as that of the divided roots. We may add, in order to complete the story of the effects of division of the dorsal roots, that the section leads to degeneration of the marginal zone (Lissauer's tract), but this degeneration reaches for a certain distance only up the cord and then disappears. It will be remembered that this zone is fed by fibres (of fine calibre) belonging to the external or lateral bundle of the dorsal roots.

These results may be interpreted as follows. The fibres of the dorsal root, cut off from their ganglion by the division, degenerate centripetally towards the spinal cord. We have previously seen that many of the fibres of the root pass into the external posterior column and run up in that column for some distance. The degeneration observed in this column for some distance above the entrance of the divided roots shews that the fibres run lengthways for some distance in this column, while the disappearance of the degeneration a little higher up similarly shews that the fibres eventually leave the column. The appearance of degeneration in the median posterior column shews that some of these fibres have passed into that column from the external posterior column, and the continuation of that degeneration right up to the bulb indicates that these fibres pursue an unbroken course in that column along the whole length of the cord. The area of degeneration, or more exactly the number of degenerated fibres in the continued tract of degeneration in the median posterior column is much less than that in the temporary or short tract of degeneration in the external posterior column. This shews that some only of the fibres passing into the external posterior column go on to join the median posterior column and so reach the bulb; the rest obviously take another path, and we have already seen reason to think that many of these end in the grey matter of the cord. Hence of all the fibres joining the cord in a dorsal root, while some, and these we may add are chiefly fine fibres, entering the grey matter directly or passing into the posterior marginal zone, soon make such connections that the degeneration due to the section of the root spreads no farther, a large number, and these chiefly coarse fibres, before they make any such connection pass into and occupy for some length of the cord the external posterior column. We may here remark that though these fibres are spread over the greater part of this column, they do not form the whole of the column; they are mixed up with fibres of a different nature and origin. Of these fibres of the dorsal root which thus run in the external posterior column while still dependent for their nutritive activity on the ganglion of the root, some, indeed the greater part, leave the tract and end by making connections in the grey matter, by forming synapses with certain cells of the grey matter; others, forming the smaller part, pass into the median posterior column, and taking up a definite position in that column pursue an unbroken course to the bulb.

All the fibres therefore of the posterior roots do not end in the grey matter soon after their entrance into the cord. A representative of each root, especially of those from the limb regions, is carried right up to the bulb by means of the median posterior column; of the axis-cylinders which leave the ganglion on the root, a certain relatively small number pursue an unbroken course for some little distance through the external posterior column, and for the rest of their way through the median posterior column, along the whole length of the cord above the entrance of the root until they find an ending in the grey matter of the bulb. Further, each spinal nerve has this representative of its posterior root placed in a definite position in the posterior median column, the arrangement being such as shewn in Fig. 107, that the lower (sacral) nerves find their place in the more dorsal and median part of the column, while the nerves above are successively placed in positions more and more ventral and external.

As far as our knowledge goes at present we are led to believe that this median posterior tract is very largely made up of fibres having this origin. It affords a channel by which centripetal impulses are carried straight up the cord from the nerve trunk without making connections on the way. We may repeat that the path is confined to the same side of the cord along its whole length; there is no crossing over to the other side.

In the above description we have spoken only of the results following section of the dorsal roots outside the cord; but it will be understood that similar results follow upon section of or injury to or disease of the cord itself affecting the posterior columns or the bundles of the roots as they enter the cord. When such a lesion occurs there may be observed in the region of the cord above the lesion a degeneration of the external posterior column, reaching some little distance up, and a more limited degeneration of a part of the median posterior column stretching right up to the bulb. The position and form of the tract of the degeneration in the median posterior column will depend on the level of the lesion along the length of the cord. according as it interrupts the ascending representatives of the sacral nerves only, or of the lumbar and sacral nerves, or of the dorsal and cervical nerves as well. A complete section or hemisection of the cord will produce results corresponding to the division on both sides or on one side of all the nerves below the section.

We may add that while, according to some observers, the strand of fibres belonging to a particular root or group of roots, having once taken up its position in the median posterior column remains unchanged until it reaches the bulb; according to others it diminishes in area, some of its fibres making connections in the cord itself.

§ **578**. The *antero-lateral ascending tract* (Fig. 107, *asc. a. l.*) is less well known than either of the two preceding; it is also more diffuse, that is to say, the fibres undergoing degeneration are more largely mixed with fibres of a different nature and origin. It appears to extend down the cord to a lower level than the cerebellar tract, but its lower limit has not yet been accurately determined. Since the degeneration taking place in it is an ascending one, it has been inferred that it serves as the path for afferent, and indeed for sensory impulses. Degeneration in it is seen only after section or injury of the substance of the cord itself, not after division of the dorsal roots. If, then, it is to be regarded as a channel of centripetal impulses passing into it from the dorsal roots, those impulses must pass into it along those fibres of the dorsal root which end by making connections with cells in some part of the grey matter; in this respect this tract resembles the cerebellar tract, and differs from the median posterior tract. The latter is the direct continuation up the cord to the bulb of such fibres as are still trusting for their nutritive activity to the cells of the ganglion on the dorsal root; the fibres of both the former trust for their nutritive activity to some or other of the nerve-cells in the grey matter of the cord. The antero-lateral ascending tract, however, does not, like the cerebellar tract, pass to the cerebellum along the restiform body; it may be traced, ventral to the restiform body, forwards along the bulb beyond which rising dorsally it turns back to the cerebellum by the superior peduncle.

§ 579. We may now briefly pass in review, somewhat as follows, the chief facts which we have learnt concerning the structure of the spinal cord, always keeping in view their physiological meaning.

The important feature of the spinal cord is the presence of what we have called 'grey matter,' and all our knowledge goes to shew that the important powers of the spinal cord, by which it differs from a thick multiple nerve, and by virtue of which we speak of it as a nervous centre or series of centres, are in some way or other associated with this grey matter.

Of this grey matter the nerve-cells (or as some call them the neurons) form the essential part, each nerve-cell consisting of a nucleus, a perikaryonic body, dendrites and an axon.

If we bear in mind that in the spinal nerves (and a like statement may be made concerning the cranial nerves) the efferent fibres are the prolonged axons of cells lying within the spinal cord, and that in the case of the afferent fibres, the peripheral portion of the fibre stretching from the cell in the ganglion of the root to the skin or other structures may be considered as the dendritic portion, though no branching occurs until close to the periphery, while the central portion between the ganglion and the spinal cord may be considered as the axon though it does not branch or give off collaterals until it has entered the cord,—if we bear these things in mind and assume that the cells or part of cells inside the cord have the same fundamental properties as those outside the cord we seem justified in making the following statement.

Though when a nerve-fibre, whether axon or dendrite, is artificially stimulated at any part of its course, the impulse thus generated travels in both directions (cf. § 72) we have reason to think that impulses which the cell carries naturally travel in one direction only, namely to the perikaryon along the dendrites and away from the perikaryon along the axon. This seems to be connected with what appears to be the case that while the whole substance of the cell, dendrites, perikaryon and axon, is eminently conductive, that is to say, readily propagates along itself a change once started in it, the part of the cell forming the terminal portions of the dendrites is eminently receptive, that is to say, changes or impulses are readily originated in those portions by disturbances in their neighbourhood, by vibrations we may perhaps say impinging upon them. Under natural circumstances, a change or impulse is always started at the receptive dendritic portion, and travels thence to the perikaryon and so along the axon; under natural circumstances an impulse, so far as we know, never travels in the contrary direction. Even if we suppose, as in the case of cells which are the instruments of automatic actions we seem driven to suppose, that impulses may originate in a cell independent of any extrinsic influence brought to bear on the receptive, dendritic portion, such impulses so far as we know always travel along the axon from the perikaryon and in no other direction.

When the axon thus carrying impulses from the perikaryon, is directed, as in the ventral spinal roots, from the central nervous system to extrinsic structures, to muscles and the like, the fibre to which it belongs is called an efferent fibre; when the axon, as in the dorsal roots, is directed to the central nervous system, the fibre to which it belongs is called an afferent fibre.

A nerve-cell of the grey matter of the cord is characterised by the rapid and often extreme branching of the dendrites and by the fact that the axon, even if, as is sometimes the case, it does not rapidly divide and branch off into a number of fine filaments, at least frequently gives off a number, sometimes a large number, of collaterals along its course, before it reaches its, may be distant, termination. And the distinguishing features of the spinal cord may be said to be, on the one hand, the extremely complex arrangement of the branches, dendrites and axons of the nerve-cells, and on the other hand, the numerous connections of cell with cell by means of synapses.

If we assume, and we seem to be entitled to assume, that each filament arising as a division either of a dendrite or an axon may serve as the path of a separate nervous impulse, the constitution of the grey matter may be regarded as affording opportunities for the most complex dispersion of nervous impulses. Again if we assume, and we seem entitled to assume, that each synapsis offers an opportunity for a change in the character of nervous impulses, that the impulse as it passes over from the terminal arborescence of an axon into the dendrite of another cell, starts in that dendrite an impulse having characters different from its own, the constitution of the grey matter may be regarded as affording opportunities for a very great conversion of impulses. Further, if we assume in accordance with what was said above, that in a nerve-cell the impulses travel, at least for the most part, centripetally towards the perikaryon, along the dendrites, and centrifugally away from the perikaryon, along the axon, a certain order will seem to be maintained in the complexity just spoken of.

Thus compared with a ganglion either of the dorsal root of a spinal nerve or even of the sympathetic system, the grey matter of the spinal cord presents marked complexity.

In a ganglion of the dorsal root the nerve-cell is simply placed on the course of the fibre by help of the T-piece; there is no division or branching of fibres; the fibre which issues from the ganglion is the same fibre as that which entered; and we have no reason whatever to suppose that the nerve-cell brings about any change in the nature of an impulse as it passes along the fibre through the ganglion. The ganglion certainly has neither reflex nor automatic action, nor have we evidence of the nerve-cell performing any function other than that of governing the nutrition and so maintaining the irritability of the whole fibre belonging to it.

The ganglion of the sympathetic system is somewhat more complex since we have reason to think that the cells may have much branched dendritic processes and that a nerve-fibre entering a ganglion may end by synapsis with one of the cells. But even this falls far short of the complexity of the arrangements in the spinal cord. And, as we have seen, the evidence that the ganglion of the sympathetic system can exercise reflex or even automatic functions is at least not conclusive.

The distinguishing feature of the spinal cord then is the extreme complexity in which the processes, dendrites and axons of its constituent cells are arranged; and we may infer that the special powers of the cord are in large measure dependent on this complexity. We may suppose, and indeed we probably must suppose, that what takes place in a particular cell is determined also by the intrinsic nature of the cell, that the nucleus, perikaryon, axon and dendrites are so constituted that the cell behaves in a particular way irrespective of the effect of its connections, that for instance two impulses of a like nature impinging on two cells by means of similar synapses may produce in the one cell an event of one kind, and in the other an event of another kind. Still making every allowance for this we must conclude that in the complexity of the arrangements of the cord lies the chief key to the problems of its actions.

§ **580**. Some of the structures of the cord form parts of mechanisms wherein the cord serves as an instrument of the brain. These are more simple in respect to efferent impulses descending from the brain than in respect to afferent impulses ascending to the brain.

The pyramidal tract diminishes as it descends from the bulb. We have reason to think that in the case of the crossed tract, fibres leaving the tract pass to the ventral horn and there form synapses with the cells whose axons go to form the ventral roots. Similarly fibres leaving the direct pyramidal tract cross by the anterior commissure to the ventral horn of the opposite side and there end by synapses with cells. In this way the pyramidal tract serves to carry impulses to the ventral roots of the spinal nerves. And a similar connection with the ventral roots also probably obtains in the case of the fibres forming the descending antero-lateral tract.

The arrangements in the case of the afferent impulses are more varied, and in some respects more complex. As we have seen the fibres of the dorsal roots are, at least in the case of the lower spinal nerves, continued in part in the median posterior tract as fibres which, except by such collaterals as they may give off, form no synapses with cells until they reach the spinal bulb; these provide for afferent impulses a channel which though in the spinal cord is not of it. The rest of the dorsal root does however end by forming synapses with the cells of some part of the grey matter either near or farther from the place of entrance of the root; the fibres form synapses with the cells of the vesicular cylinder, with the cells of the posterior horn and with other cells. From the cells of the vesicular cylinder axons passing into the lateral column form the cerebellar tract. Thus by a relay in the vesicular cylinder afferent impulses reaching the cord by the dorsal roots are carried up past the cord to the brain above. And by a similar relay in some cells of the grey matter, either of the vesicular cylinder or other, impulses are carried up to the brain by the fibres of the ascending antero-lateral tract.

§ **581.** Excluding these recognized tracts carrying impulses to and from the brain, with the cells of the grey matter belonging to them, the rest of the cord, unless other like tracts should hereafter be demonstrated, may be considered as supplying mechanisms belonging to the cord itself.

We have reason to think that some of the fibres of a dorsal root end, that is to say either the terminations or the collaterals of some of the fibres, end by forming synapses directly with the body or dendrites of the cells in the ventral horn whose axons go to form a ventral root. This supplies a mechanism of the simplest form whereby afferent impulses may give rise in a reflex act to efferent impulses. But we cannot suppose that this is the only mechanism by which in the cord afferent impulses are brought to bear on cells which carry out efferent impulses.

We have seen that the area of white matter immediately surrounding the grey matter on its lateral and ventral aspects consists largely of fibres which since they run a very short course in the white matter do not appear as lengthy tracts of degeneration after section or injury. These are fibres which starting as the axons of certain cells in the grey matter pass into the white matter and after running a very short course return to the grey matter where they end by forming synapses with other cells. That is to say these fibres represent a mechanism by which cells of one part of the cord affect cells in another part. We cannot at present state precisely what they do. Some of the cells to which these fibres belong, thrown into activity by impulses reaching them through afferent fibres, may carry forward impulses, which, even if modified by the relay, may still be regarded as afferent impulses; and by a series of such relays impulses, still recognisable as afferent impulses, might travel along a considerable length of the cord. Further, though still of the nature of afferent impulses, they might travel either upwards or downwards. And, in the end, after a longer or shorter course they might be brought to bear on cells sending axons into ventral roots, and so by giving rise to efferent impulses, bring about reflex actions.

Or the impulses arising in other of the cells to which these fibres belong might be from the beginning of the nature of efferent impulses, and thus efferent impulses might be conducted along the cord. Or the impulses might be of a nature which could not be considered as distinctly either efferent or afferent.

Another kind of intrinsic mechanism is also present. In the case of certain cells in the grey matter, the axon does not run a long course, passing into the white matter as a fibre, and at most giving off collaterals; it divides at once within the grey matter in a branching fashion, and speedily forms a synapsis with another cell, or it may be forms synapses with more than one cell. Such a cell serves to carry or distribute impulses within the grey matter, possibly transforming those impulses in some way as it carries them.

Thus, after all the structures connecting the cord with the brain have been excluded, the remaining grey matter, either with or without the help of the intraspinal fibres of the white matter, presents a mechanism of great complexity for the passage of impulses along, and their possible transformation within the cord. With this both afferent dorsal and efferent ventral roots are connected, and the complexity of the whole mechanism will appear all the greater when it is remembered that each axon entering into the mechanism may bear collaterals, and that the synapses effected by these may be different from that in which the axon itself ends, and may be different from each other. We may infer that this mechanism or parts of it are concerned in carrying out the functions which the cord is capable of performing by itself without the intervention of the brain.

Lastly, the two lateral halves of the cord are bound together by numerous transverse commissural ties, by fibres or their collaterals, or by naked axons, or possibly in some cases by elongated dendrites. By means of these, impulses entering into or passing along one side of the cord are brought to bear on structures of the other side.

SEC. 3. THE REFLEX ACTIONS OF THE SPINAL CORD.

§ **582**. In the preceding portions of this work we have repeatedly seen that though we can learn much concerning the working of an organ, or tissue or part of the body by studying its behaviour when isolated from the rest of the body, all the conclusions thus gained have to be checked by a study of the behaviour of the same organ or part, while it is still an integral part of the intact body. All the several organs and tissues are so bound together by various ties, that the actions of each depend on the actions of the rest; and to say that the life of each part is a function of the life of the whole, is no less true than to say that the life of the whole is a function of the life of each part. This is especially borne in upon us, when we come to study the actions of the central nervous system. We may, on anatomical grounds, separate the spinal cord from the brain; but when we come to consider the respective functions of the two, we are brought face to face with the fact that in actual life a large part of the work of the brain is carried out by means of the spinal cord, and conversely the spinal cord does its work habitually under the influence of, if not at the direct bidding of the brain. We may gain certain conclusions by studying the behaviour of the spinal cord isolated from the brain, or of parts of the spinal cord isolated from each other; but we must be even more cautious than when we were dealing with other parts of the body, and must greatly hesitate to take it for granted that the work which we can make the spinal cord or a part of the spinal cord do, when isolated from the brain, is the work which is actually done in the intact body when the brain and spinal cord form an unbroken whole. Moreover this caution becomes increasingly necessary, when in our studies we pass from the simpler nervous system of one animal to the more complex nervous system of another; for it is by the complexity of their central nervous systems more than by any thing else, that the 'highest' animals are differentiated from those 'below' them.

When we compare a rabbit, a dog, a monkey and a man, the differences in the vascular, digestive and respiratory systems of the four, striking as they may appear, sink into insignificance compared with the differences exhibited by their respective central nervous systems. We need caution when from the results of experiments on dogs or rabbits, we draw conclusions as to the digestion or circulation of man, but we need far greater caution when from the behaviour of the isolated spinal cord of one of these animals we infer the behaviour of the intact spinal cord of man.

A further difficulty meets us when an experimental investigation entails operative interference with the central nervous system. Removal or section of, or other injury to parts of the brain or spinal cord is very apt to give rise in varying degree to what is known as 'shock.' The cutting or tearing or other lesion of any considerable mass of nervous substance affects the activity, not only of the structures immediately injured, but of other, it may be far distant, structures. The nature of 'shock' is not as yet thoroughly understood, but may perhaps, in part at all events, be explained by regarding the lesion as a very powerful stimulus, which, partly by way of inhibition but still more by way of exhaustion, depresses or suspends for a while normal functions, and thus gives rise to temporary diminution or loss of consciousness, of volition, of reflex movements and other nervous actions. Thus a section through the spinal cord, even when made with the sharpest instrument and with the utmost skill, so as to avoid all bruising as much as possible, may for a while suspend all reflex activity of the cord, or indeed all the obvious activities of the whole central nervous system. We may add that such a 'shock' of the central nervous system may also be produced by sudden lesions not bearing directly on the central nervous system, as for instance by extensive injury to a limb.

Moreover in many cases in which the effects of experimental interference have been watched for some considerable time, days, months or years after the operation, it has been observed, on the one hand, that phenomena which are conspicuous in the early period may eventually disappear, and, on the other hand, that activities which are at first absent may later on make their appearance; movements for instance which are at first frequent after a while die away, and conversely, movements which at first seemed impossible are later on easily achieved. We have to distinguish or to attempt to distinguish between the temporary and the lasting effects of the operation, including among the former not only those of ordinary 'shock,' but others of slower development or longer duration. In many instances where a part of the central nervous system is by section or otherwise suddenly separated from the rest, the phenomena suggest that the separated part is at first profoundly influenced as to its activities by the withdrawal of various influences which previously were being exerted upon it by the rest of the system, but later on accommodates itself to its new conditions, and learns, so to speak, to act without the help of those influences. And indeed it is possible that some of the effects of even immediate 'shock' may be due, not, as suggested above, to the action of an inhibitory or exhausting stimulus, but to the sudden cessation of habitual influences.

Still, in spite of all these difficulties, it is possible not only to ascertain the working of an isolated portion of the central nervous system, but even to infer from the results some conclusions as to the share taken by that portion in the working of the entire and intact system. There can be no doubt, for instance, that the spinal cord can, quite apart from the brain, carry out various reflex actions, and that moreover it does carry out actions of this kind when in the intact organism it is working in concert with the brain. Indeed the carrying out of various reflex actions seems to be one of the most important functions of the spinal cord, so much so that, though the brain or, at least, parts of the brain can also and do develope reflex actions, the spinal cord offers the best field for the study of these actions. We have already (§ 101) touched on the general features of reflex actions, and elsewhere have incidentally dwelt on particular instances; we may therefore confine ourselves now to certain points of special interest.

§ **583**. Reflex movements are perhaps best studied in the frog and other cold-blooded animals, since in these the actions of the cord are less dependent on, and hence less obscured by the working of, the other parts of the central nervous system. They obtain however in the warm-blooded mammal also, but in these special precautions are necessary to secure their full development. In the frog the shock, which as we have said follows upon division of the spinal cord and for a while suspends reflex activity, soon passes away; within a very short time after the bulb for instance has been divided the most complicated reflex movements can be carried on by the frog's spinal cord when the appropriate stimuli are applied. With the mammal the case is very different. For days even after division of the spinal cord the parts of the body supplied by nerves springing from the cord below the section may exhibit very feeble reactions only. In the dog, for instance, after division of the spinal cord in the lower dorsal region, the hind limbs hang flaccid and motionless, and pinching the hind foot evokes as a response either slight irregular movements or none at all. Indeed were our observations limited to this period we might infer that the reflex actions of the spinal cord in the mammal were but feeble and insignificant. If however the animal be kept alive for a longer period, for weeks or better still for months, though no union or regeneration of the spinal cord takes place, reflex movements of a powerful, varied and complex character manifest themselves in the hind limbs and hinder parts of the body; a very feeble stimulus applied to the skin of these regions promptly gives rise to extensive and yet coordinate movements. Indeed the more the matter is studied, the stronger is the evidence that the reflex movements carried out by isolated portions of the spinal cord of the mammal are hardly less definite, complete and purposeful, than those witnessed in the frog. It is worthy of attention, as bearing out the remarks made above on the great differentiation of the central nervous system in the higher animals, that the reflex phenomena in mammals vary very much not only in different species but also in different individuals and in the same individual under different circumstances. Race, age, and previous training, seem to have a marked effect in determining the extent and character of the reflex actions which the spinal cord is capable of carrying out; and these seem also to be largely influenced by passing circumstances, such as whether food has been recently taken or no. It has been asserted that the isolated spinal cord of the rabbit, which has been the subject of so many experiments, is, as compared with that of the dog and many other mammals, singularly deficient in the power of carrying out complex reflex movements.

In studying reflex actions in man we are met with the difficulty that we never have to deal with a portion of the spinal cord separated from the rest of the central nervous system under the favourable circumstances of experimental investigation. In man, we must be content to examine reflex actions either while the whole nervous system is intact, or when a portion of the cord has been wholly or partially separated by some more or less diffuse disease or by some accident involving more or less crushing of the nervous structures. Hence, the caution already given, as to drawing inferences concerning man from the results of experiments on animals, acquires still greater force.

§ **584**. Confining ourselves at first to the results of experiments on animals we may say that in both cold-blooded and warm-blooded animals the salient feature of ordinary reflex actions is their purposeful character, though every variety of movement may be witnessed, from a simple spasm to a most complex manœuvre. And in all reflex movements, both simple and complex, we can recognize certain determining influences which more or less directly contribute to the shaping of this purposeful character.

Thus the features of any movement taking place as part of a reflex action are in part determined by the characters of the afferent impulses. Simple nervous impulses generated by the direct artificial stimulation of afferent nerve-fibres generally evoke as reflex movements merely irregular spasms in a few muscles; whereas the more complicated differentiated sensory impulses generated by the application of the stimulus to the skin, readily give rise to large and purposeful movements. It is easier to produce a complex reflex action by a slight pressure on or other stimulation of the skin than by even strong induction-shocks applied directly to a nerve trunk. If, in a brainless frog, the area of skin supplied by one of the dorsal cutaneous nerves be separated by section from the rest of the skin of the back, the nerve being left attached to the piece of skin and carefully protected from injury, it will be found that slight stimuli applied to the surface of the piece of skin easily evoke reflex actions, whereas the trunk of the nerve may be stimulated with even strong currents without producing anything more than irregular movements. In ordinary mechanical and chemical stimulation of the skin it is not a single impulse but a series of impulses which passes upwards along the sensory nerve, the changes in which may be compared to the changes in a motor nerve during tetanus. In every reflex action, in fact, the central mechanism may be looked upon as being thrown into activity through a summation of the afferent impulses reaching it. Hence while a reflex action is readily called forth by even feeble induction-shocks applied to the skin if they be repeated sufficiently rapidly, a solitary induction-shock is ineffectual unless it be strong enough to cause in the skin or nerves changes of an electrolytic nature sufficient to give rise of themselves to a series of impulses.

§ 585. When a muscle is thrown into contraction in a reflex action, the pitch of the sound which it gives forth does not vary with the stimulus, but is constant, being the same as that given forth by a muscle thrown into contraction by the will. From which we infer, even bearing in mind the discussion in § 80 concerning the nature of the muscular sound, that in a reflex action the afferent impulses do not simply pass through the centre in the same way that they pass along afferent nerves, but are profoundly modified. And in accordance with this we find, as we shall see, that a reflex action takes up an amount of time, the greater part of which is spent in the carrying out of the central changes, and which though variable is always much longer, and may be very much longer, than that taken up by the mere passage of a nervous impulse along a corresponding length of nerve-fibre. The term reflex action is therefore an unsuitable one. The afferent impulse is not simply reflected or turned aside into an efferent channel; on its arrival at the centre it starts changes of a different nature from and more complex than its own; and the issue of efferent impulse is the result of those more complex changes, not the mere continuation of the simpler afferent impulse. In other words, the interval between the advent at the central organ of afferent, and the exit from it of efferent impulses, is a busy time for the nervous substance of that organ; during it many processes, of which we have at present very little exact knowledge, are being carried on.

§ 586. The character of the movement forming part of a reflex action is also influenced by the intensity of the stimulus. A slight stimulus, such as gentle contact of the skin with some body, will produce one kind of movement; and a strong stimulus, such as a sharp prick applied to the same spot of skin, will call forth quite a different movement. When a decapitated snake or newt is suspended and the skin of the tail lightly touched with the finger, the tail bends towards the finger; when the skin is pricked or burnt, the tail is turned away from the offending object. And so in many other instances. It must be remembered of course that a difference in the intensity of the stimulus entails a difference in the characters of the afferent impulses; gentle contact gives rise to what, when the brain takes part in the action, we call a sensation of touch, while a sharp prick gives rise to pain, consciousness being differently affected in the two cases because the afferent impulses are different. Hence the instances in question are in reality fuller illustrations of the dependence, to which we called attention above, of the characters of a reflex movement on the characters of the afferent impulses.

Further, as we have already pointed out (§ 101), while the motor impulses started by a weak stimulus applied to an afferent nerve are transmitted along a few, those started by a strong stimulus may spread to many efferent nerves. Granting that any particular afferent nerve is more especially associated with certain efferent nerves than with any others, so that the reflex impulses generated by afferent impulses entering the cord by the former pass with the least resistance down the latter, we must evidently admit further that other efferent nerves are also, though less directly, connected with the same afferent nerve, the passage into the second efferent nerve meeting with a greater but not an insuperable resistance. When a frog is poisoned with strychnia, a slight touch on any part of the skin may cause convulsions of the whole body; that is to say, the afferent impulses passing along any single afferent nerve may give rise to the discharge of efferent impulses along any or all of the efferent nerves. This proves that a physiological though, as we have seen, not an anatomical continuity obtains between all the parts of the spinal cord which are concerned in reflex action, that the nervous arrangement intervening between the afferent and efferent fibres forms along the whole length of the cord a functionally continuous field. This continuous field however we must suppose to be marked out into tracts presenting greater or less resistance to the progress and transformation of the impulses. We have seen (§ 569) that the fibres of a dorsal root effect synapses with cells whose axons go to form a ventral root. This is the simplest form of a reflex mechanism, the one in which there is the least resistance, the impulse along the afferent filament impinging on the dendrite or body of the efferent cell, and so directly giving rise to impulses along the efferent (motor) axon. If, as seems to be the case, the fibres in one dorsal root may thus make direct connections, not only with the cells belonging to the fibre of its fellow ventral root but also to those of roots above or even below, the path to the fibres of the fellow ventral root may still be considered as offering less resistance than do the other paths; this would seem to follow from the distance to be travelled, even if there were no other determining influences. But a dorsal root makes direct connections of this kind with at most a few of the nearest ventral roots; the connections of that dorsal root with other ventral roots is an indirect one, one carried out by the relay of some cell or other of the grey matter; and the introduction of this relay will greatly increase the resistance. With still more distant ventral roots, more than one such cell may be introduced as a relay into the chain, and the resistance still further increased. And so on. Without insisting too much on this view we may accept it as suggesting an explanation of how the path of any impulse, and so its effects, may be determined by its initial energy. On the other hand we may suppose that some change in the condition of the filaments and cells of the chain might so reduce the resistance that even weak impulses should travel over the whole of it with great ease, and may thus explain the action of the strychnia.

§ **587.** Further, the movement, forming part of a reflex action, varies in character according to the particular part of the body to which the stimulus is applied. The reflex actions developed by stimulation of the internal viscera are different from those excited by stimulation of the skin. We have reason to think that the contraction of or other changes in a skeletal muscle may produce, by reflex action, contractions of other muscles; and such reflex actions also differ from those started by stimulation of the skin. In reflex actions started by applying a stimulus to the skin the movements vary largely according to the particular area of the skin which is affected. Thus, pinching the folds of skin surrounding the anus of the frog produces different effects from those witnessed when the flank or toe is pinched; and, speaking generally, the stimulation of a particular spot calls forth particular movements. In the case of the simpler reflex movements, it appears to be a general rule that a movement started by the stimulation of a sensory surface or region on one side of the body, is developed on the same side of the body, and if it spreads to the other side, still remains most intense on the same side; the movement on the other side moreover is symmetrical with that on the same side. It has been maintained that 'crossed' or diagonal reflex movements, as where stimulation of one fore-foot leads to movements of the opposite hind-limb, do not occur unless some portion of the bulb be left attached to the spinal cord. Seeing that locomotion in four-footed animals is largely effected by diagonal movements of the limbs, one would rather have expected to find the spinal cord itself provided with mechanisms to assist in carrying them out;

and indeed it is affirmed that in the case of cold-blooded animals and of many young mammals, after division of the spinal cord below the bulb, a gentle stimulation will provoke a diagonal movement, slight pressure on one fore-foot for example giving rise to movements in the opposite hind-leg; a strong stimulus however will produce an ordinary one-sided movement. Again, when in a dog the cord has been divided in the lower thoracic region so that the hind limbs depend on the lumbar cord alone, a rhythmically repeated drawing up and letting down of the hind limbs is witnessed when these are allowed to hang down; and these movements, which appear to be of a reflex nature excited by the pendant position of the limbs, are often seen to alternate regularly in the two limbs, the right leg being extended while the left leg is being drawn up and vice versa. It may further be observed that if the foot of one pendant limb be pinched while the other limb is passively flexed the flexion of the limb which is pinched is accompanied by an extension of the other limb. In these respects however different animals, as already urged, differ from each other.

§ **588.** From these and similar phenomena we may infer that the nervous field spoken of above is, so to speak, mapped out into nervous mechanisms by the establishment of lines of greater or less resistance, so that the disturbances in it generated by certain afferent impulses are directed into certain efferent channels. It may be added that though conspicuously purposeful movements seem to need the concurrent action of several segments of the cord, and, as a rule, the greater the length of the cord involved the more complex and the more distinctly purposeful the movement, still the movements evoked by even a segment of the cord may be purposeful in character; hence we must conclude that every segment of the nervous field is mapped out into mechanisms. But the arrangement of these mechanisms, especially of the more complex ones, is not a fixed and rigid one. We cannot always predict exactly the nature of the movement which will result from the stimulation of any particular spot, because the result will vary according to the condition of the spinal cord, especially in relation to the strength and character of the stimulus. Moreover, under a change of circumstances a movement quite different from the normal one may make its appearance. Thus when a drop of acid is placed on the right flank of a brainless frog, the right foot is almost invariably used to rub off the acid; in this there appears nothing more than a mere 'mechanical' reflex action. If however the right leg be cut off, or the right foot be otherwise hindered from rubbing off the acid, the left foot is, under the exceptional circumstances, used for the purpose. This at first sight looks like an intelligent choice. A choice it evidently is; and were there many instances of choice, and were there any evidence of a variable automatism, like that which we call 'volition,' being manifested by the spinal cord of the frog, we should be justified in supposing that the choice was determined by an intelligence. But, as we shall have occasion later on to point out, a frog, deprived of its brain so that the spinal cord only is left, makes no spontaneous movements at all. Such an entire absence of spontaneity is wholly inconsistent with the possession of intelligence. Then again the above experiment, if not the only instance, is at all events by far the most striking instance of choice on the part of a brainless frog. We are therefore led to conclude that the phenomena must be explained in some other way than by being referred to the working of an intelligence. Moreover this conclusion is supported by the behaviour of other animals. Thus similar vicarious reflex movements may be witnessed in mammals, though not perhaps to such a striking extent as in frogs. In dogs, in which partial removal of the cerebral hemispheres has apparently heightened the reflex excitability of the spinal cord, the remarkable scratching movements of the hind leg which are called forth by stimulating a particular spot on the loins or side of the body, are executed by the leg of the opposite side, if the leg of the same side be gently held. In this case the vicarious movements are ineffectual, the leg not being, as in the case of the frog, crossed over so as to bear on the spot stimulated, and cannot be considered as betokening intelligence. Again, the 'mechanical' nature of reflex actions is well illustrated by the behaviour of a decapitated snake. When the body of the animal in this condition is brought into contact at several places at once with an arm or a stick, complex reflex movements are excited, the obvious purpose as well as effect of which is to twine the body round the object. A decapitated snake will however with equal and fatal readiness twine itself round a red-hot bar of iron, which is made to touch its skin in several places at the same time.

§ **589**. In considering the nature of the events in the spinal cord which determine the behaviour of the frog in the instance just mentioned we must bear in mind that the movements in question are 'coordinated;' that is to say, not only are many distinct muscles brought into play but certain relations are maintained between the amount, duration, and exact time of occurrence of the contraction of each muscle and those of the contractions of its fellow muscles sharing in the movement. In the absence of such coordination the movement would become irregular and ineffectual. We shall have occasion later on in dealing with voluntary movements to point out that the coordination, and hence the due accomplishment of a voluntary movement is dependent on certain afferent impulses passing up from the contracting muscles to the central nervous system, and guiding the discharge of the efferent impulses which call forth the contractions. When these afferent impulses affect consciousness we speak of them as constituting a 'muscular sense;' it is, as we shall see, by the 'muscular sense' that we become aware of and can appreciate the condition of our muscles. But we have reason to think that the afferent impulses which constitute the basis of the muscular sense, whatever be their exact nature, in order to play their part in bringing about the coordination of a voluntary movement need not pass right up to the brain and develope a distinct muscular 'sense,' but may produce their effect by working on the nervous mechanisms of the spinal cord with which the motor fibres carrying out the movement are connected. In other words, the coordination of a voluntary movement takes place in the part of the spinal cord which carries out the movement, and not in the brain, though the latter may be conscious of the whole movement including its coordination.

But if the spinal cord possesses mechanisms for carrying out coordinated movements, which in the case of voluntary movements are discharged by nervous impulses descending from the brain, we may infer that in reflex actions the same mechanisms are brought into action though they are discharged by afferent impulses coming along afferent nerves instead of by impulses descending from the brain. The movements of reflex origin, in all their features except their exciting cause, appear identical with voluntary movements; the two can only be distinguished from each other by a knowledge of the exciting cause. And it seems unreasonable to suppose that the spinal cord should possess two sets of mechanisms in all respects identical save that the one is discharged by volitional impulses from the brain and the other by afferent impulses from afferent nerves.

We are led therefore to the conclusion that in a reflex action carried out by the cord two kinds of afferent impulses are concerned: the ordinary afferent impulses which start the movement, which discharge the nervous mechanism within the cord and so provoke the movement, and the afferent impulses which connect that nervous mechanism with the muscles about to be called into play, and which take part in the coordination of the movement provoked. The nature of these latter afferent impulses is at present obscure; we know as yet little more than the fact of their existence; but if we admit, as we seem compelled to do, that the character of a reflex action is determined by them as well as by the afferent impulses which actually discharge the mechanism, it seems possible that a fuller knowledge of these coordinating afferent impulses may afford an adequate explanation of the fact that when, as in the case of the frog in question, the usual set of muscles cannot be employed by the nervous mechanism, recourse is had to another set.

We have avoided the introduction of the word 'consciousness' as unnecessarily complicating the question; and it would be out of place to discuss psychological problems here. We may remark however that since we have no objective proofs of consciousness outside ourselves, and only infer by analogy that such and such an act is an outcome of consciousness on account of its likeness to acts which are the outcome of our own consciousness, we conclude that the brainless frog possesses no active consciousness like our own, because absence of spontaneous movements seems to be irreconcilable with the existence of an active consciousness whose very essence is a series of changes. Consciousness as we recognize it seems to be necessarily operating as, or to be indissolubly associated with the presence of, an incessantly repeated internal stimulus; and we cannot conceive of that stimulus failing to excite mechanisms of movement which, as in the case of the brainless frog, are confessedly present. We may however distinguish between an active abiding consciousness, such as we usually understand by the term, and a passing or momentary condition, which we may speak of as consciousness, but which is wholly discontinuous from an antecedent or from a subsequent similar momentary condition; and indeed we may suppose that the complete consciousness of ourselves, and the similarly complete consciousness which we infer to exist in many animals, has been gradually evolved out of such a rudimentary consciousness. We may, on this view, suppose that every nervous action of a certain intensity or character is accompanied by some amount of consciousness, which we may, in a way, compare to the light emitted when a combustion previously giving rise to invisible heat waxes fiercer. We may thus infer that when the brainless frog is stirred by some stimulus to a reflex act, the spinal cord is lit up by a momentary flash of consciousness coming out of darkness and dying away into darkness again; and we may perhaps further infer that such a passing consciousness is the better developed the larger the portion of the cord involved in the reflex act and the more complex the movement. But such a momentary flash, even if we admit its existence, is something very different from consciousness as ordinarily understood, is far removed from intelligence, and cannot be appealed to as explaining the 'choice' spoken of above.

§ 590. Lastly, the characters of a reflex movement are, as we need hardly say, dependent on the intrinsic condition of the cord. The action of strychnia just alluded to is an instance of an apparent augmentation of reflex action best explained by supposing that the resistances in the cord are lessened. There are probably however cases in which the explosive energy of the nervous substance is positively increased above the normal. Conversely, by various influences of a depressing character, as by various anæsthetics or other poisons, reflex action may be lessened or prevented; and this again may arise either from an increase of resistance, or from a diminution in the actual discharge of energy. So, also, various diseases may so affect the spinal cord as to produce on the one hand increased reflex excitability, so that a mere touch may produce a violent movement, and on the other hand diminished reflex excitability, so that it becomes difficult or impossible to call forth a reflex action.

§ **591**. When we come to study the reflex actions of man we should at first perhaps be inclined to infer that, since in him the spinal cord is so largely used as the instrument of the brain, the independent reflex actions of the cord, at least such as affect skeletal muscles, are in him of much less importance than they appear to be in animals; and experience seems to support this view. But it must be remembered that in his case, as we have already stated (§ 583), we lack the guidance of experimental results; we are obliged to trust to the entangled phenomena of disease or to a study of the behaviour of the cord while it is still a part of an intact nervous system; and each of these methods presents difficulties of its own. The movements, which in the intact human body we can recognize as indubitable reflex actions, are as a rule simple and unimportant. They are, in by far the greater number of instances, occasioned by stimulation of the skin or of the mucous membrane, for the most part involve a few muscles only, and rarely indicate any very complex coordination. The flexion, followed by extension, of the leg which is called forth by tickling the sole of the foot, or the winking of the eye when the cornea or conjunctiva is touched, may perhaps be regarded as the type of these movements. A very common form of reflex action is that in which a muscle or group of muscles is thrown into contraction by stimulation of the overlying or neighbouring skin, as when the abdominal muscles contract upon stroking the skin of the abdomen or the testicle is retracted upon stroking the inside of the thigh. A reflex movement may occur as the result of stimulation of an organ of special sense, parts of the central nervous system other than the spinal cord serving as the centre. A sound or a flash of light readily produces a start, a bright light makes the eye wink and may cause a person to sneeze (the greater coordination manifest in this act being due to the fact that the complex respiratory mechanism is brought into play, § 391), and reflex movements may result from a taste or smell. An action resembling at least a reflex action, is called forth by sharply striking certain tendons; for instance striking the tendon below the patella gives rise to a sudden extension of the leg, known as the 'knee-jerk'; but it will be best to discuss these tendon reactions or 'tendon reflexes,' as they are often called, later on in another connection.

On the whole the reflex movements carried out by the intact nervous system of man are, we repeat, scanty and comparatively simple; and the same features characterize the reflex movements carried out by the cord or by parts of the cord which are witnessed in various diseases.

In some stages of certain diseases of the spinal cord extensive reflex movements are witnessed; but these are not purposeful coordinated movements, such as have been described above as occurring in frogs and mammals after experimental interference, but rather mere exaggerations of the simpler reflex movements witnessed when the nervous system is intact. In cases of paraplegia (such being the term generally used when disease or injury has cut off the cord, generally the lower part of the cord, from the brain so that the will cannot bring about movements in, and the mind derives no sensations from, the parts below the lesion, the legs for instance), it sometimes happens that contact with the bedclothes, or other external objects, sets up from time to time rhythmically repeated movements, the legs being alternately drawn up and thrust out again. It is rarely if ever that reflex movements of a really complicated character are observed. Moreover clinical experience shews that in man, when a portion of the cord is isolated, reflex actions carried out by means of that portion so far from being exaggerated are much oftener exceedingly feeble or absent altogether. In the cases in which the physiological continuity of the lower with the upper part of the cord has been broken by disease, by some growth invading the nervous structures or by some changes of the nervous structures themselves, we may attempt to explain the absence from the lower part of coordinate reflex activity, such as is seen in the lower animals, as due to the disease not only affecting the powers of the actually diseased part, but influencing the whole cord below, and either by inhibition, of which we shall speak presently, or in some other way depressing its functions. But the same absence of complex reflex movements is also often observed in cases in which the cord has been severed by accident, and indeed, though accidental injuries to the human cord generally produce more profound and extensive mischief than that which results in animals from skilful experimental interference, clinical experience reveals only simple and scanty reflex actions, and so tends, on the whole, to support the view that in man the more complete subordination of the spinal cord to the brain has led to the dying out of the complex reflex actions which are so conspicuous in the lower animals.

Moreover a like absence of complex purposeful spinal reflex movements is met with also in monkeys; and that even when the experimental interference has been carried out with the greatest care. For instance, when the spinal cord has been divided in a monkey in the thoracic region, the reflex movements which can be evoked in the lower limbs are remarkably scanty and simple.

We must not however therefore conclude that the nervous mechanisms for carrying out varied reflex movements are absent from man and the monkey, though present in the dog and the frog. We may suppose that in the former animals the effects, which we have spoken of as those of 'shock,' are more lasting and more profound than in the latter, and further that in the former the spinal mechanisms, owing to the close functional dependence of the spinal cord on the brain in these animals, suffer in some way and lose their activity upon separation from the brain before the effects of shock have passed away. And that such spinal mechanisms are present is suggested by the following considerations.

When we come to study voluntary movements we shall see reason to think that in man, as in the lower animals, the will in carrying out these movements makes use of complex nervous mechanisms situated in the spinal cord, nervous mechanisms into the working of which, as urged above, afferent impulses enter largely; and it seems improbable that these spinal mechanisms should be capable of being thrown into action by the will only. In the act of walking for instance it is highly probable that the movements of the legs are the direct results of the action of nervous mechanisms in the lumbar cord; the will simply brings these mechanisms into play and the movements are thus, in an indirect manner only, the products of volitional impulses. And even though clinical and experimental experiences only afford us instances in man and in the monkey of this machinery working apart from the brain in a damaged condition or at least under unfavourable circumstances so that the resemblance of the movements observed to the complete act of walking is but feeble, still it seems probable that under more favourable circumstances the lumbar cord separated from the brain might as part of a reflex act carry out the movements in a more complete and coordinate manner.

§ 592. We have dwelt above chiefly on reflex actions, in which the efferent impulses cause contractions of skeletal muscles since these are undoubtedly the most common and the most prominent forms of reflex action; but it must not be forgotten that the efferent impulses of reflex origin may produce contractions of other muscles, as well as other effects, such as secretion for instance. On several of these we have dwelt from time to time in previous parts of this work, and it will be unnecessary to repeat them here. But it may be worth while to point out that the spinal cord by serving as a reflex centre for innumerable ties which correlate the nutritive or metabolic activities of the several tissues to events taking place in other parts of the body, plays a conspicuous part in securing the welfare of the whole body. In dealing (§ 549) with the general problems of nutrition, we stated that an orderly nutrition appears to be in some way dependent on nervous influences. Many of these nervous influences appear to issue from the spinal cord, either as parts of a reflex act, or as the outcome of some automatic processes. When in a dog the lumbar cord is wholly separated from the rest of the cord by section, the nutrition of the hind limbs, and the general health of the animal may, with care, be maintained in a very satisfactory condition; but if that small separated piece of the cord be destroyed death inevitably ensues before long, in spite of every care and precaution, being brought about apparently by the disordered nutrition of the hind limbs and other parts supplied by nerves coming from the lumbar cord. In man, extensive injuries to the spinal cord are followed by bed-sores and other results of impaired nutrition; and indeed death is generally brought about in this way, in cases of paraplegia caused by accidental crushing or severance of the cord. The scarcity of well-marked reflex actions mentioned above as characteristic of such cases, may perhaps be due to the fact that these disorders of nutrition prevent the patient living long enough for the separated cord to recover the functions which properly belong to it.

§ **593**. *Inhibition of Reflex Action.* The reflex actions of the spinal cord, like other nervous actions, may be totally or partially inhibited, that is to say, may be arrested or hindered in their development by impulses reaching the centre while it is already in action. Thus if the body of a decapitated snake be allowed to hang down, slow rhythmic pendulous movements, which appear to be reflex in nature, soon make their appearance, and these may be for a while arrested by slight stimulation, as by gently stroking the tail. We have already seen that the action of such nervous centres as the respiratory and vaso-motor centres, which frequently at all events is of a reflex nature, may be either inhibited or augmented by afferent impulses. The micturition centre in the mammal, which is also largely a reflex centre, may be easily inhibited by impulses passing downward to the lumbar cord from the brain, or upward along the sciatic nerves. In the case of dogs, whose spinal cord has been divided in the thoracic region, micturition set up as a reflex act by simple pressure on the abdomen or by sponging the anus, is at once stopped by sharply pinching the skin of the leg. And it is a matter of common experience that in man micturition may be suddenly checked by an emotion or other cerebral event. The erection centre in the lumbo-sacral cord, also in large measure a reflex centre, is similarly susceptible of being inhibited by impulses reaching it from various sources. In the monkey when the spinal bulb is left in connection with the spinal cord, the rest of the brain having been removed, peculiar long-continued reflex movements may be easily evoked by an appropriate stimulus; thus when the finger is dipped in hot water the whole arm is bent, brought forward and kept in that position for some time; but a pinch of the ear at once arrests the movement and brings down the arm again. And indeed many similar instances of the inhibition of reflex movements might readily be quoted.

Several apparent instances of the inhibition of reflex acts are not really such: in these cases all the nervous processes of the act may take place in their entirety and yet fail to produce their effect on account of a failure in the muscular part of the act.

Thus when we ourselves by an effort of the will stop the reflex movements which otherwise would be produced by tickling the soles of the feet, we achieve this to a large extent by throwing voluntarily into action certain muscles, the contractions of which antagonise the action of the muscles engaged in carrying out the reflex movements. But it may be doubted, even in these cases, whether inhibition is always or wholly to be explained in this way; and certainly in very many instances of reflex inhibition, no such muscular antagonism is present, and the reflex act is checked at its nervous centre.

When the brain of a frog is removed, and the effects of shock have passed away, reflex actions are developed much more readily and to a much greater degree than in the entire animal, and in mammals also reflex excitability has been observed to be increased by removal of the cerebral hemispheres. This suggests the idea that in the intact nervous system the brain is habitually exerting some influence on the spinal cord tending to prevent the normal development of the spinal reflex actions. And we learn by experiment that stimulation of certain parts of the brain has a remarkable effect on reflex action. If a frog, from which the cerebral hemispheres have been removed (the optic lobes, bulb and spinal cord being left intact), be suspended by the jaw, and the toes of the pendent legs be from time to time dipped into very dilute sulphuric acid, a certain average time will be found to elapse between the dipping of the toe and the resulting withdrawal of the foot. If, however, the optic lobes or optic thalami be stimulated, as by putting a crystal of sodium chloride on them, it will be found on repeating the experiment while these structures are still under the influence of the stimulation, that the time intervening between the action of the acid on the toe and the withdrawal of the foot is very much prolonged. That is to say, the stimulation of the optic lobes has caused impulses to descend to the cord, which have there so interfered with the nervous processes engaged in carrying out reflex actions as greatly to retard the generation of efferent impulses, or in other words, has inhibited the reflex action of the cord. And similar results may be obtained in mammals by stimulating certain parts of the corpora quadrigemina, which bodies are homologous to the optic lobes of frogs. From this it has been inferred that there is present in this part of the brain a special mechanism for inhibiting the reflex actions of the spinal cord, the impulses descending from this mechanism to the various centres of reflex action being of a specific inhibitory nature. But, as we have already seen, impulses of an ordinary kind, passing along ordinary sensory nerves, may inhibit reflex action. We have quoted instances where a slight stimulus, as in the pendulous movements of the snake, and where a stronger stimulus, as in the case of the micturition of the dog, may produce an inhibitory result;

we may add that in the frog adequately strong stimuli applied to any afferent nerve will inhibit, *i.e.* will retard or even wholly prevent reflex action. If the toes of one leg are dipped into dilute sulphuric acid at a time when the sciatic of the other leg is being powerfully stimulated with an interrupted current the period of incubation of the reflex act will be found to be much prolonged, and in some cases the reflex withdrawal of the foot will not take place at all. And this holds good, not only in the complete absence of the optic lobes and bulb, but also when only a portion of the spinal cord, sufficient to carry out the reflex action in the usual way, is left. There can be no question here of any specific inhibitory centres, such as have been supposed to exist in the optic lobes. But if it is clear that inhibition of reflex action may be brought about by impulses which are not in themselves of a specific inhibitory nature, we may hesitate to accept the view that a special inhibitory mechanism in the sense of one giving rise to nothing but inhibitory impulses is present in the optic lobes of frogs, and after removal of the brain that the exaltation of reflex actions which is manifest is due to the withdrawal of such a specific inhibitory mechanism.

The presence of the brain does obviously produce an effect which may be broadly spoken of as inhibitory, and a specific action of the brain, in an effort of the will, may stop or inhibit a specific reflex action; but we must not in these matters be led too much away by the analogy of the special and limited cardiac inhibitory mechanism. There we have apparently to deal with fibres, whose exclusive duty it is to convey inhibitory impulses from the bulb to the cardiac muscle, and inhibition of the heart, at least through nervous influences, is exclusively carried out by them. But already, in studying the nervous mechanism of respiration, we have seen reason to think that afferent impulses passing along the same nerves, and probably along the same fibres, may, according to circumstances, now inhibit, now augment the respiratory centre, and have thus been led to speak of inhibitory impulses, that is impulses producing an inhibitory effect, apart from specific inhibitory fibres. In the complex working of the central nervous system, we may still more expect to come across similar instances of the same channels serving as the path, either of inhibition or of augmentation. In all probability, actions or processes, which we may speak of as inhibitory, do play, as indeed we shall see, an important part in the whole work of the central nervous system; we shall meet with instances almost immediately when we come to deal with 'tone' in relation to the spinal cord. In all probability many of the phenomena of nervous life are the outcome of a contest between what we may call inhibitory and exciting or augmenting forces; but in all probability also we ought rather to seek for the explanation of how vagus impulses inhibit the beat of the heart by reference to the inhibitory phenomena of the central nervous system, than to attempt to explain the latter by the little we know of the former. At present, however, we must be content with the fact that experiments on animals shew that the brain, not only by some action or other may inhibit particular spinal reflex movements, but also habitually exercises a restraining influence on the reflex activity of the whole cord, though we are unable to state clearly how this inhibition is carried out.

We say 'experiments on animals' because though we know, as stated above, by an appeal to our own consciousness, that an action of the brain, an effort of the will, may stop a particular reflex act, we have no evidence that in man separation of the cord from the brain leads, as in animals, to heightened reflex activity. In diseases, or injuries to the cord, reflex actions are, as we have said, sometimes exaggerated, but it is possible and indeed probable that the increase is due to the morbid processes producing a greater irritability of the cord itself, and not to the withdrawal of any inhibitory influences. In many cases, in perhaps the greater number, no exaggeration but a diminution or even absence of reflex activity is observed; so much so that could we trust explicitly to clinical experience, we should be inclined to conclude that the scantiness of spinal reflex action in man was due not to any preoccupation of the cord by influences proceeding from a dominant brain, but to an inherent paucity of spinal reflex mechanisms. But we have already said all we have at present to say on this point.

§ **594**. *The Time required for Reflex Actions.* When one eyelid is stimulated with a sharp electrical shock, both eyelids blink. Hence, if the length of time intervening between the stimulation of the right eyelid and the movement of the left eyelid be measured, this will give the total time required for the various processes which make up a reflex action. It has been found to be from ·0662 to ·0578 sec. Deducting from these figures the time required for the passage of afferent and efferent impulses along the fifth and facial nerves to and from the bulb, and for the latent period of the contraction of the obicularis muscle, there would remain ·0555 to ·0471 sec. for the time consumed in the central operations of the reflex act. The calculations, however, necessary for this reduction, it need not be said, are open to sources of error; moreover the reflex act in question is carried out by the bulb and not by the spinal cord proper. Blinking thus produced is a reflex act of the very simplest kind; but as we have seen in the preceding pages, reflex acts differ very widely in nature and character; and we accordingly find, as indeed we have incidentally mentioned, that the time taken up by a reflex movement varies very largely. This indeed is seen in blinking itself. When the blinking is caused not by an electric shock applied to the eyelid, but by a flash of light falling on the retina, in which case complex visual processes are involved, the time is distinctly prolonged; moreover the results in different experiments in which light serves as the stimulus are not nearly so uniform as when the blinking is caused by stimulation of the eyelid.

In general it may be said that the time required for any reflex act varies to a great extent with the strength of the stimulus employed, being less for the stronger stimuli. So far as we know all impulses whether started by a weak or by a strong stimulus travel along a nerve fibre at the same rate; hence the quickening of the whole reflex act with the stronger impulse must be due to increased facility of transference at the synapses or more rapid action in the cell-bodies of the nerve-cells concerned. It is stated that when the movement induced is on the same side of the body as the surface stimulation of which starts the act, the time taken up is less than when the movement is on the other side of the body, allowance being made for the length of central nervous matter involved in the two cases; that is to say, the central operations of a reflex act are propagated more rapidly along the cord than across the cord. The rapidity of the act varies of course with the condition of the spinal cord, the act being greatly prolonged when the cord becomes exhausted; and a similar delay has been observed in cases of disease. The time thus occupied by purely reflex actions must not be confounded with the interval required when the changes taking place in the central nervous system are of a more complicated nature, and more or less distinctly involve mental operations; of the latter we shall speak later on.

SEC. 4. THE AUTOMATIC ACTIONS OF THE SPINAL CORD.

§ 595. We speak of an action of an organ or of a living body as being spontaneous or automatic when it appears to be not immediately due to any changes in the circumstances in which the organ or body is placed, but to be the result of changes arising in the organ or body itself and determined by causes other than the influences of the circumstances of the moment. Some automatic actions are of a continued character; others, like the beat of the heart, are repeated in regular rhythm; but the most striking automatic actions of the living body, those which we attribute to the working of the will and which we call voluntary or volitional, are characterized by their apparent irregularity and variableness. Such variable automatic actions form the most striking features of an intact nervous system, but are conspicuously absent from a spinal cord when the brain has been removed.

A brainless frog placed in a condition of complete equilibrium in which no stimulus is brought to bear on it, protected for instance from sudden passing changes in temperature, from a too rapid evaporation by the skin and the like, remains perfectly motionless until it dies. Such apparently spontaneous movements as are occasionally witnessed are so few and seldom, that we can hardly do otherwise than attribute them to some stimulus, internal or external, which has escaped observation. In the mammal (dog) after division of the spinal cord in the dorsal region regular and apparently spontaneous movements may be observed in the parts governed by the lumbar cord. When the animal has thoroughly recovered from the operation the hind limbs rarely remain quiet for any long period; they move restlessly in various ways; and when the animal is suspended by the upper part of the body, the pendent hind limbs are continually being drawn up and let down again with a monotonous rhythmic regularity, suggestive of automatic rhythmic discharges from the central mechanisms of the cord. In the newly-born mammal too, after removal of the brain, movements apparently spontaneous in nature are frequently observed. But all these movements, even when most highly developed, are very different from the movements, irregular and variable in their occurrence though orderly and purposeful in their character, which we recognize as distinctly voluntary. Even admitting that some of the movements of the brainless mammal may resemble voluntary movements in so far as they are due to changes taking place in the spinal cord itself independent of the immediate influence of any stimulus, we are not thereby justified in speaking of the spinal cord as developing a will in the sense that we attribute a will to the brain.

§ 596. In the case of the beat of the heart, the automatic rhythmic discharge of energy appears to be exclusively the outcome of the molecular nutritive changes taking place in the cardiac substance. The beat may be modified, as we have seen, by nervous impulses reaching the cardiac substance along certain nerves; but the actual existence of the beat is wholly independent of these extraneous influences; the rhythmic discharge continues when they are entirely absent. The automatic rhythmic discharge of respiratory impulses from the respiratory centre is also dependent on the intrinsic molecular changes of the centre, these being, as we have seen, largely determined by the character of the blood streaming through it; but in this case extrinsic nervous impulses, reaching the centre along the vagus and other nerves, play a much more important part than do similar impulses in the case of the heart. They act so continually on the centre and enter so largely into its working, that we are compelled to regard the activity of the centre as fed, if we may use the word, not only by the intrinsic molecular nutritive processes of the centre itself, but also by the extrinsic nervous influences which flow into the centre from without. The automatism of the spinal cord as a whole resembles, in this aspect, that of the respiratory centre rather than that of the heart. It has for its basis doubtless the intrinsic molecular changes of the grey matter, on whose remarkable constitution we dwelt in a previous section; the metabolic events of this substance are so ordered as to give rise to discharges of energy; but the discharge appears to be also intimately dependent on the inflow into the grey matter of afferent impulses and influences. The normal discharge of efferent impulses from the cord undoubtedly takes place under the influence of these incoming impulses; and it may be doubted whether the grey matter of the cord would be able, in the absence of all afferent impulses, to generate any sustained series of discharges out of its merely nutritive intrinsic changes. The automatic activity of the cord is fed not only by intrinsic nutritive events, but also by extrinsic influences.

In this feature we may, moreover, find perhaps the reason why the automatic activity of the spinal cord is so limited, as compared with that of the brain. In spite of certain striking but superficial characters of which we shall speak later on, the grey matter of the brain presents no histological features so different from those of the grey matter of the cord, as to justify us in concluding that the one is capable and the other incapable of developing the impulses, which we call volitional, out of the molecular nutritive changes of its substance. We are, therefore, led to the conclusion that the fuller automatic activity of the brain is due to the intrinsic changes of its substance being so much more largely assisted by the influx of various afferent impulses and influences, notably those of the special senses. To this question, however, we shall have to return later on.

§ **597**. In treating of the vascular system we saw that the central nervous system exercised through the vaso-motor nerves such an influence on the muscular coats of the blood vessels as to maintain, what we spoke of as 'tone,' section of vaso-constrictor fibres leading to "loss of tone." We saw further, that arterial tone, though normally dependent on the general vaso-motor centre in the bulb, could be kept up by the cord itself, that for instance a tone of the blood vessels of the hind-limbs could be maintained by the isolated thoraco-lumbar cord. This maintenance of arterial tone may be spoken of as one of the "automatic" functions of the spinal cord. We have also seen that plain muscular fibres, other than those of the arteries, notably the fibres forming sphincters, such as the cardiac and pyloric sphincters of the stomach, the sphincter of the bladder, and especially the sphincter of the anus, also possess tone, and that the tone of these sphincters is also dependent on the spinal cord, or on some part of the central nervous system. We need not repeat the discussions concerning these mechanisms and other instances of the spinal cord exercising an automatic influence over various viscera; we have referred to them here, since they serve as an introduction to a question which has been much debated, and which has many collateral and important bearings, namely the question whether the spinal cord exercises an automatic function in maintaining a tone of the skeletal muscles.

The question is not one which, like the case of arterial tone, can be settled off hand by a simple experiment. Some observers maintain that the section of a motor nerve does not produce any clearly recognizable immediate lengthening of a muscle supplied by the nerve, in the same way that section of a vaso-constrictor nerve undoubtedly gives rise to a relaxation of the muscular fibres in the arteries governed by it; and it has been inferred from this that skeletal tone does not exist. But others have observed such a lengthening; and there are several facts to be taken into consideration before we can come to a just decision.

The skeletal muscles have been described as being placed "on the stretch" in the living body. If a muscle be cut away from its attachments at each end, it shortens; if it be cut across, it gapes.

In other words, the muscle in the living body possesses a latent tendency to shorten, which is continually being counteracted by its disposition and attachments. In studying muscular contraction we saw (§ 87) that the shortening of a contraction is followed by a relaxation or return to the former length, both the contraction and relaxation being the result of molecular changes in the living muscular substance. We have now to extend our view and to recognize that, apart from the occurrence of ordinary contractions, molecular changes are by means of nutritive processes continually going on in the muscle in such a way that the muscle, though continually on the stretch, does not permanently lengthen, but retains the power to shorten upon removal or lessening of the stretch, and conversely though possessing this power of shortening permits itself to lengthen when the stretch is increased. In this way the muscle is able to accommodate itself to variations in the amount of stretch to which it is from time to time subjected. When a flexor muscle for instance contracts, the antagonistic extensor muscle is put on an increased stretch and is correspondingly lengthened; when the contraction of the flexor passes off the extensor returns to its previous length; and so in other instances. Thus by virtue of certain changes within itself a muscle maintains what may be called its natural length in the body, always returning to that natural length both after being shortened and after being stretched. In this the muscle does no more than do the other tissues of the body which, within limits, retain their natural form under the varied stress and strain of life; but the property is conspicuous in the muscle; and its effects in skeletal muscles correspond so closely to those of arterial tone, that we may venture to speak of it as skeletal tone. Indeed, the molecular changes at the bottom of both are probably the same.

These changes are an expression of the life of the muscle; they disappear when the muscle dies and enters into rigor mortis; and moreover, during life they vary in intensity so that the 'tone' varies in amount according to the nutritive changes going on. We have seen reason to believe that the nutrition of a muscle as of other tissues is governed in some way by the central nervous system. We saw, in treating of muscle and nerve (§ 83), that the irritability of a muscle is markedly affected by the section of its nerve, *i.e.* by severance from the central nervous system; and again (§ 549) in speaking of the so-called trophic action of the nervous system, we referred to changes in the nutrition of muscles occasioned by diseases of the nervous system. And experience, especially clinical experience, shews that the nutritive changes which determine tone are very closely dependent on a due action of the central nervous system. When we handle the limb of a healthy man, we find that it offers a certain amount of resistance to passive movements. This resistance, which is quite independent of, that is to say, which may be clearly recognized in the absence of all distinct muscular contractions of volitional or other origin, is an expression of muscular tone, of the effort of the various muscles to maintain their 'natural' length. In many cases of disease this resistance is felt to be obviously less than normal; the limb is spoken of as "limp" or "flabby;" or as having 'a want of tone.' In other cases of disease, on the other hand, this resistance is markedly increased; the limb is felt to be stiff or rigid; more or less force is needed to change it from a flexed to an extended, or from an extended to a flexed condition; and, in the range of disease, we may meet with very varying amounts of increased resistance, from a condition which is only slightly above the normal to one of extreme rigidity. In some cases the condition of the muscle is such as at first sight seems much more comparable to a permanent ordinary contraction than to a mere exaggeration of normal tone; but all intermediate stages are met with; and indeed these extreme cases may be taken as indicating that the molecular processes which maintain what we are now calling tone, are at bottom, of the same nature as those which carry out a contraction; they serve to shew the fundamental identity of the skeletal tone with the more obvious arterial tone.

Clinical experience then shews that the central nervous system does exert on the skeletal muscles such an influence as to give rise to what we may speak of as skeletal tone, changes in the central nervous system, leading in some cases to diminution or loss of tone, in other cases to exaggeration of tone, manifested often as conspicuous rigidity. The question why the changes take one direction in one case and another in another is one of great difficulty (the occurrence of extreme rigidity being especially obscure), and cannot be discussed here. We have called attention to the facts simply because they shew the existence of skeletal tone and its dependence on the central nervous system. This conclusion is confirmed by experiments on animals, and these also afford proof that in animals the spinal cord can by itself, apart from the brain, maintain the existence of such a tone. In a frog, after division of the cord below the brain, the limbs during the period of shock are flabby and toneless; but after a while, as the shock passes off, tone returns to the muscles, and the limbs offer when handled a resistance like that of the limbs of an entire frog. When the animal is suspended the hind limbs do not hang perfectly limp and helpless, but assume a definite position; and that this position is due to some influence proceeding from the spinal cord is shewn by dividing the sciatic nerve on one side; the hind limb on that side now hangs quite helpless. This more pendent position shews that some of the flexors have lengthened in consequence of the section of the nerve, and this result may be taken as refuting the argument, quoted above against the existence of tone, which is based on the statement that a muscle cannot be observed to lengthen after section of its nerve. It may be here remarked that if the brainless frog, whose hind-limbs are more or less pendent when the body is suspended, be placed on its belly the hind-limbs are brought into a flexed position under the body by means of obvious muscular contraction; and from this it might be inferred that the maintenance of the position of the pendent limb was also the result of a feeble contraction. But no obvious contractions can be observed in the latter case, as in the former; and when in the former the limb has once been brought into the flexed position, that position, like the pendent position, is maintained without obvious contractions. As we said above 'tone' may pass into something which appears to be identical with a contraction, but where no obvious contractions are observed it seems preferable to speak of the state of the muscle as one of tone.

In the dog, after division of the cord in the thoracic region, the hind-limbs during the period of shock are limp and toneless. In the warm-blooded animal, as we have said, the effects of shock are much more lasting than in the cold-blooded animal; and in the dog the tone of the skeletal muscle returns much more slowly than in the frog. Indeed when the division of the cord has taken place low down the skeletal tone returns very slowly, and may be manifested very feebly, or even be absent altogether. But under favourable circumstances, when a sufficient length of cord has been left, a fairly normal tone is reestablished. In man, in accordance with the facts previously mentioned (§ 591) skeletal tone, which has been lost through the continuity of the cord being broken by disease or accident, appears rarely if ever to return fully in the regions below the lesion.

We may therefore on the whole of the evidence conclude that the maintenance of skeletal tone is one of the functions of the cord; but we may here repeat that the condition of the cord, on which depends the issue from the cord along efferent nerves of the influences, whatever their nature, which produce tone in the muscle, may be, and indeed is, in its turn dependent on afferent impulses. In the case of the frog quoted above the tone of the pendent limbs disappears or is greatly lessened when the posterior roots of the sciatic nerves are divided, though the anterior roots be left intact. In the absence of the usual stream of afferent impulses passing into it, the cord ceases to send forth the influences which maintain the tone. Hence the maintenance of tone presents many analogies with a reflex action, especially when we remember that, as stated above, tone passes insensibly into contraction; and it may seem a mere matter of words whether we speak of the maintenance of tone as an automatic or as a reflex action of the cord. We may, however, distinguish the part played by the afferent impulses in assisting the cord to a condition in which it is capable of maintaining tone from the part played by an afferent impulse in causing a reflex action; in the former the action of the afferent impulses seems analogous to that of a supply of arterial blood in maintaining an adequate irritability of the nervous substance, in the latter the afferent impulses lead directly to a discharge of energy. And it is convenient to distinguish the two things by different names.

§ 598. The close connection between tone and reflex action is illustrated by the so-called 'tendon-phenomena,' which, on the one hand, have been considered as cases of ordinary reflex action, and, on the other hand, may be, and more justly, regarded as exemplifying a special influence of the spinal cord on the irritability and so the 'tone' of the muscles.

It is well known that when the leg is placed in an easy position, resting for instance on the other leg, a sharp blow on the patellar tendon will cause a sudden jerk forward of the leg, brought about by a contraction of the extensor muscles of the thigh. Similarly the muscles of the calf may be thrown into action by tapping the tendo Achillis put somewhat on the stretch by flexion of the foot; and in some cases the same muscles may be made to execute a series of regular rhythmic contractions, called 'clonic' contractions, by suddenly pressing back the sole of the foot so as to put them on the stretch. The contraction of the muscles of the thigh produced by tapping the patellar tendon, and familiarly known as the 'knee-jerk,' has been investigated in much detail and may, with profit, be considered at some length. The main facts are as follows:

The jerk is brought about by a contraction of the vastus internus and of part of the crureus division of the quadriceps extensor muscle (Fig. 111, *Va. Cr*). For its development the presence and functional activity of certain nervous structures are necessary; and these as in a reflex act consist of a chain of three factors, namely: (1) efferent fibres running in the anterior crural nerve, and leaving the cord in the monkey (in which animal the act has been experimentally studied) by the ventral roots of the 4th and 5th lumbar (subthoracic) nerves (3rd and 4th in man); (2) a spinal centre situate in the monkey in the 5th and 4th lumbar segments; and (3) afferent fibres, reaching the spinal cord in the monkey by the dorsal root of the 5th lumbar nerve (4th lumbar in man), and arising in the vastus internus and crurens muscles. If any one of these three parts of the chain be interfered with, if the above ventral roots be divided, or the centre injured, or the dorsal root in question be divided, the jerk is abolished: tapping the tendon no longer brings about the contraction. Further, the readiness and the vigour of the response to the tap is modified by such conditions of the spinal cord, or of the whole central nervous system, or of the body at large as usually modify reflex actions; thus the jerk is diminished, is wholly or partially inhibited in certain nervous diseases and by some influences, such as sleep, and is augmented, reinforced in other nervous states and by other influences, such as vigorous movements of other parts of the body.

All this looks very much as if the act were simply an ordinary reflex act. But a difficulty presents itself. If the time which elapses between the blow on the tendon and the beginning of the movement be measured this is found to be very short, ·02 sec., far shorter than that of any known reflex act; and indeed if the measurement be made between the tap and the very beginning of the contraction of the muscular fibres themselves (as may be done by a special arrangement), the interval is actually less than that which occurs when the contraction is brought about by stimulating the motor nerve at some distance from the muscle. It seems impossible, in view of this fact, to regard the act as a reflex act; and we are led to the conclusion that the contraction is idio-muscular, is brought about by the vibrations started in tendon running up to the muscle and directly stimulating the muscular fibres, and not by nervous impulses making the reflex circuit through the spinal cord. But if so, we are at the same time led also to the conclusion, that the irritability of the muscle, its

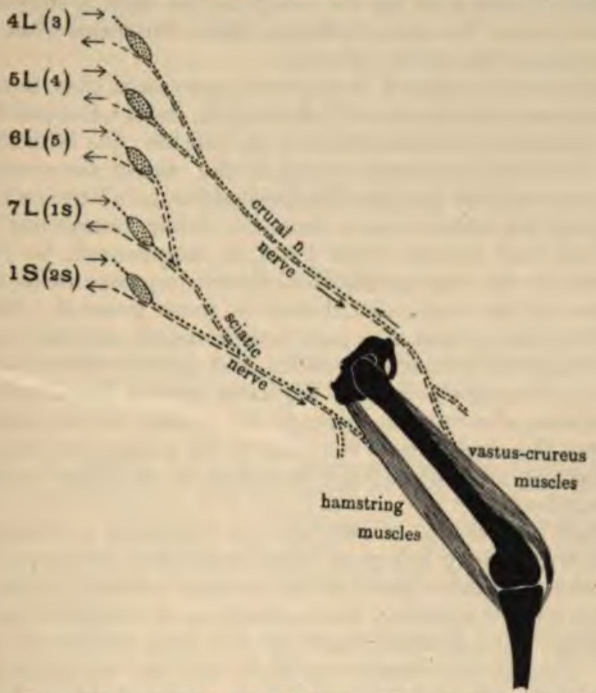


FIG. 111. DIAGRAM ILLUSTRATING THE NERVOUS MECHANISM OF THE KNEE-JERK.

4 *L*, 5 *L*, 6 *L*, the roots of the 4th, 5th, and 6th lumbar nerves in the monkey (Macacus); the corresponding roots in man (indicated in brackets) are the 3rd, 4th and 5th. 7 *L*, the 7th lumbar in the monkey corresponding to the 1st sacral in man. 1 *S*, 1st sacral in the monkey, 2nd sacral in man. In both crural and sciatic nerves the efferent path is indicated by a broken, and the afferent by a dotted line.

readiness to respond to the vibrations, is closely dependent on the spinal cord, that the spinal cord is continually exerting an influence on the irritability of the muscle. Such an influence is the basis of the tone which we are discussing; and the dependence of that irritability, of that tone, on the integrity not only of efferent fibres and of the centre but also of afferent fibres illustrates what we said just now about the nature of tone.

Further, it is a matter of common experience that to obtain a favourable result in the way of a knee-jerk, the tendon and extensor muscle should be put somewhat on the stretch; the limb should be flexed. Now, experimental study, in the case of the monkey, has shewn that the jerk may on the one hand be inhibited by impulses passing up the sciatic nerve from the flexor, hamstring muscles (Fig. 111), and on the other hand be augmented, be rendered more brisk by preventing the flow of such impulses, as by dividing the fibres of the sciatic distributed to those muscles. Similarly, though to a less extent, the jerk is diminished, partially inhibited by stretching the hamstring muscles, and augmented by slackening them, as in flexing the knee. We have here an instance in which the condition of a muscle, through the agency of the spinal cord, influences the condition of the tone of its antagonist muscle; for the hamstring muscles and the extensors of the thigh are antagonistic muscles.

Indeed the study of the various instances of antagonistic muscles in the body brings to light increasing evidence that the spinal cord (and other parts of the central nervous system) influences the tone of muscles; the contraction of a muscle has for its concomitant an inhibition (more or less pronounced) of its antagonist. Thus in the movements of the eye, the contraction of one rectus muscle (internal or external) is associated with an inhibition of its antagonist rectus (external or internal). It would seem that the 'tone' of skeletal muscles and its regulation, inhibition or augmentation, plays a not unimportant part in the due carrying out of the various movements of the body.

§ **599**. Disease in man reveals occasionally other conditions of the skeletal muscles which sometimes take on the form of extreme rigidity, of exaggerated tone, and sometimes of rhythmic 'clonic' contractions. These may at times superficially resemble reflex actions, and have been spoken of by some authors as 'muscle reflexes.' Though the spinal cord plays its part in their production they seem to be essentially due to causes originating in some parts or other of the brain, and are too obscure to be dwelt on here.

It remains for us to speak of the part played by the spinal cord, as the instrument of the brain, in the execution of voluntary movements and in the development of conscious sensations; but it will be best to consider these matters in connection with the brain itself, to the study of which we must now turn.

CHAPTER II.

THE BRAIN.

SEC. 1. ON SOME GENERAL FEATURES OF THE STRUCTURE OF THE BRAIN.

§ 600. IT would be out of place to attempt to give here a complete description of the structure of the brain; but certain features must be kept fresh in the mind as a basis for physiological discussion; and to these we must now turn our attention, a general acquaintance with the topographical anatomy of the brain being presupposed[1].

Like the spinal cord the brain consists of 'white matter,' in which the nervous elements are almost exclusively medullated fibres, and of 'grey matter,' in which nerve-cells and other nervous elements are also present; but the grey matter of the brain is much more variable in structure than that of the spinal cord, and possesses features peculiar to itself; these we shall study later on.

For physiological purposes the brain may be conveniently divided into parts corresponding to the divisions which appear in it in the embryo. At an early stage in the life of the embryo that part of the medullary tube which is about to become the brain differs from that which is about to become the spinal cord, in that the central canal, which in the latter is of fairly uniform bore along its whole length, is in the former alternately widened and narrowed, so that the tube forms a series of vesicles, the cerebral vesicles, succeeding each other lengthways. At first these vesicles are three in number, called respectively fore-brain, mid-brain, and hind-brain; but the fore-brain after having developed on each side a lateral vesicle, the optic vesicle, subsequently transformed into the retina and optic nerve, gives rise in front of itself to a pair of vesicles placed side by side, or rather to a single vesicle with a deep median furrow, the vesicle of the cerebrum, containing a cavity divided by a median partition into two cavities, lying side by side, which open into the cavity of the original fore-brain by a Y-shaped opening. This embryonic chain of vesicles is developed into the adult brain by unequal growth of the walls and unequal expansion of the cavities, certain features being also impressed upon it by the bend on the longitudinal axis, which takes place in the region of the mid-brain and is known as the cranial flexure.

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[1] Figs. 112 onwards, which will be found in succeeding sections, may with advantage be consulted in reading this section though not specially referred to in the text.

§ 601. In the hind part of the hinder vesicle or hind-brain, the ventral, basal portion or floor is thickened to form the *bulb*, while the greater part of the dorsal portion or roof does not thicken at all, is not transformed into nervous elements, but remains as a single layer of epithelium, adherent to the pia mater overlying it, and so forms a thin covering to the lozenge-shaped cavity of the vesicle, now known as the *fourth ventricle*.

In the front part of the same hind-brain, on the contrary, the roof and sides are enormously developed into the conspicuous *cerebellum* overhanging the front part of the fourth ventricle, while the floor is also thickened into the *pons Varolii*.

This thickening of the pons is largely made up on the one hand of horizontal nerve-fibres, which run transversely from each side of the cerebellum into the pons, and on the other hand of longitudinal fibres, which run forwards from the bulb and are wrapped round by and interlaced with the others. At the front margin of the pons these longitudinal fibres, augmented in number, appear as two thick strands, the *crura cerebri*, forming the floor of the mid-brain, the roof of which is thickened into the *corpora quadrigemina*, and the cavity of which is reduced to a narrow tubular passage, the *aqueduct of Sylvius*, or *iter a tertio ad quartum ventriculum*.

At the level of the fore-brain the crura cerebri, diverging rapidly from each other as they pass forwards, leave the median portion of the floor of the vesicle now known as the *third ventricle* very thin, but form, especially behind and ventrally, thick lateral walls, which are further increased in thickness by the development on each side of a mass largely composed of grey matter, known as the *optic thalamus*. The roof of the third ventricle, like that of the fourth ventricle, is not developed into nervous elements but remains extremely thin, and consists of nothing more than a single layer of epithelium.

§ 602. In front of the third ventricle each diverging crus cerebri spreads out into a radial fashion into the corresponding half of the paired vesicle of the cerebrum now developed into the preponderant *cerebral hemispheres*, the two cavities of which are now known as the *lateral ventricles*. The growth of the cerebral hemispheres is not only much greater than that of the rest of the brain, but also takes place in a special manner. At their first appearance the cerebral hemispheres lie wholly in front of the fore-brain or vesicle of the third ventricle, but in their subsequent growth, while expanding in nearly all directions, they extend especially backwards. Thus in the adult brain, on the dorsal surface they not only completely cover up the third ventricle but also overlap the mid-brain, reaching so far back as to cover the front border of the cerebellum, while on the ventral surface, though in the middle line they leave exposed the floor or ventral portions of the walls of the third ventricle, at the sides they are seen to reach as far backward as on the dorsal surface. The median furrow on the dorsal surface which separates each hemisphere from its fellow is at first shallow but rapidly deepens, so that as the hemispheres grow they become separated from each other by a narrow deep longitudinal fissure, into which as we shall see a fold of the dura mater dips. This fissure is not only deep vertically, *i.e.* from the dorsal surface ventrally, but at the front of the brain runs backward in the middle line almost as far as the level of the third ventricle, so as completely to separate from each other the anterior parts of each hemisphere, known as the anterior lobes; at the back of the brain also it similarly runs forward in the middle line for a considerable distance, so as to separate from each other the posterior lobes. Hence the two great masses of the cerebral hemisphere are united with each other, not along their whole length but for about a third of that length, the isthmus or bridge thus connecting them lying at some depth below the dorsal surface at the bottom of the longitudinal fissure, in about the middle third of its length.

At its first appearance each lateral ventricle is of a more or less oval form, its walls are of uniform thickness, and it lies in front of the third ventricle. During the growth of the hemispheres it acquires a peculiar shape and becomes divided into an anterior cornu or horn stretching into the anterior portion, a posterior horn stretching into the posterior portion, and a descending horn, which curves laterally and ventrally into the middle portion of the hemisphere; owing to the great backward extension of the hemispheres the lateral ventricles come to lie not only in front of but also at the side of, and indeed, to a certain extent, above or dorsal to the third ventricle; and during the growth of the parts the originally wide Y-shaped opening which placed the hind ends of the two lateral ventricles in communication with the front of the third ventricle becomes narrowed into a slit-like passage of similar form, the foramen of Monro, which still opening into the front of the third ventricle, now leads on each side from a point rather in front of the middle of the lateral ventricle.

As the hemisphere enlarges the growth of the walls of the vesicle is not uniform in all parts. At an early period there may be observed in the ventral wall or floor of the vesicle a thickening, which assuming a special, more or less semilunar, form and projecting into the cavity becomes the body known as the *corpus striatum*. As development proceeds the corpus striatum on each side becomes attached to the optic thalamus, lying behind and to the median side of itself, the radiating fibres of the crus cerebri passing between the two, and also as we shall see dividing the corpus striatum into two bodies, called the *nucleus caudatus* and *nucleus lenticularis*. A notable result of this growth and change of position of the hemispheres and of the coalescence of the corpus striatum with the optic thalamus is that the latter body, though really belonging to the third ventricle, comes to project somewhat into the lateral ventricle; a strip of the upper surface of the optic thalamus, along its outer, lateral edge, forms a portion of the floor of the lateral ventricle in the median region on each side of the third ventricle. Besides this special development of the corpus striatum, the walls of each vesicle, with the exception of the median part by which the two vesicles coalesce with each other, become (we are now speaking of the higher mammals) thickened much in the same way all over, the surface being folded so as to give rise to convolutions or *gyri* separated by furrows or *sulci;* and the thickening takes place in such a manner as to give the ventricle its peculiar shape. The median coalesced part undergoes a different and peculiar change. This part, which at first lies in front of the third ventricle, through the changes brought about by the growth of the hemispheres so shifts its position as to lie immediately over, dorsal to the third ventricle, very much as if this part of the cerebral vesicles had been folded back over the fore-brain. In the junction itself we may distinguish a dorsal and a ventral portion. The dorsal portion is developed into a system of transverse commissural fibres passing across from one hemisphere to the other. In the median region these fibres form a thick compact band, called the *corpus callosum*, which may be exposed to view at the bottom of the longitudinal fissure, while on each side they spread away in all directions to nearly all parts of the surface of the hemispheres, passing over and helping to form the roof of the lateral ventricles. The band is not flat but curved ventralwards; hence in a longitudinal vertical section of the brain taken in the middle line it presents a curved form with the concavity directed ventralwards. While this dorsal portion of the junction is developed at the sides as well as in the middle line, the ventral portion is developed in the median region only, and that in a special way, so that it forms below, ventral to, the corpus callosum an arched plate, in the shape of a triangle with the apex directed forwards, called the *fornix*, which lies immediately above the thin epithelial roof of the third ventricle. In front, the narrower apical portion of the fornix lies at some little distance below, ventral to, the corpus callosum, and here the junction between the two vesicles is reduced to a thin sheet, the *septum lucidum;* but behind, the broader basal portion of the fornix is arched up so as to lie immediately under and touch the corpus callosum. Hence the septum lucidum has the form of a more or less triangular vertical sheet, broad in front and narrowing behind, separating the two lateral ventricles. The sheet may be conceived of as being double and formed by the apposition of two layers, one belonging to each ventricle; between these two layers is developed a narrow closed cavity containing fluid, called the *fifth ventricle.* But while the lateral ventricles open by the foramen of Monro into the third ventricle and the third ventricle is continuous by means of the aqueduct with the fourth ventricle, which again passes into the central canal of the spinal cord, the whole series being developed out of the same embryonic neural canal, the fifth ventricle communicates with none of them; it is a cavity of different origin.

The corpus callosum or dorsal portion of the junction between the vesicles spreads out, as we have said, laterally along its whole length, and thus forms a broad band joining the two hemispheres together; the middle portion spreads out in a more or less straight direction, though curving over the ventricle upwards and downwards to reach various parts of the hemisphere, while the front and hind ends bend round on each side forwards and backwards to reach the anterior and posterior parts. Thus through the corpus callosum the thick wall of one ventricle is made continuous with that of the other. The disposition of the fornix or ventral portion of the junction is very different. At its apex in front the fornix bifurcates into two bands, known as the pillars of the fornix, which on each side become continuous with, and take a peculiar course in the walls of the third ventricle. In like manner behind, the angles of the base of the fornix are continuous with the walls of the lateral ventricles, that is to say, with the thick mass of the hemispheres, being also prolonged as two special strands of fibres called the crura of the fornix. But along each side of the triangle, between the attachments in front and behind, the substance of the fornix is not continued into the substance of the corresponding hemisphere; the edge of the fornix appears on each side to lie loose on the dorsal surface of the optic thalamus, which here forms the median portion of the floor of the lateral ventricle; between the optic thalamus below and the fornix above there seems to be a narrow slit by which the cavity of the lateral ventricle communicates with parts outside itself. In reality however there is no actual breach of continuity though there is a breach of nervous substance. The slit is bridged over by a layer of epithelium, by means of which the edge of the fornix is made continuous with the upper surface of the optic thalamus, and the median wall of the lateral ventricle made complete. But this layer of epithelium has the following peculiar relations to the pia mater covering the brain.

We have said that the roof of the third ventricle, like that of the fourth ventricle, consists only of a layer of epithelium devoid of nervous elements. We have further seen that the fornix, and the hind part of the corpus callosum with which it is continuous overlie the third ventricle, the free base of the fornix with the rounded hind end of the corpus callosum above forming together the hind border of the junction or bridge between the two hemispheres. The pia mater covering the dorsal surface of the brain, passing forwards under this curved border, spreads over the top of the third ventricle, becoming adherent to the layer of epithelium just referred to, and thus forms a vascular sheet called the *velum interpositum*, which serves as the actual roof of the third ventricle, immediately below, ventral to, the fornix; it cannot be seen without previously removing the fornix. At the lateral edge of the fornix, on each side, this same vascular sheet of pia mater projects from beneath the fornix into the lateral ventricle carrying with it the layer of epithelium, which, as we said, made the edge of the fornix actually continuous with the rest of the walls of the lateral ventricle; the part of the pia mater thus seen projecting beyond the edge of the fornix when the lateral ventricle is laid open is called the *choroid plexus*. To this peculiar intrusion of the pia mater, by which the nutrition of the brain is assisted, we shall return when we come to speak of the vascular arrangements of the brain. Meanwhile we may point out, that while this vascular ingrowth seems to make the cavity of the third ventricle continuous with that of the lateral ventricle on each side, and all three with the exterior of the brain, it really does not do so. The cavity of the third ventricle is made complete by the layer of epithelium forming its roof, and the cavity of the lateral ventricle is made complete by the layer of epithelium passing from the lateral edge of the fornix over the choroid plexus to the other parts of the wall of the ventricle. To pass along this line from the actual cavity of the lateral into that of the third ventricle one must first pierce the epithelium covering the choroid plexus, thus gaining access to the pia mater of the plexus and of the velum, and then again pierce the epithelium coating the under surface of the velum and forming the roof of the third ventricle. It is only by the foramen of Monro that a real communication exists between the cavity of the lateral and that of the third ventricle.

Thus by the large growth and backward extension of the cerebral hemispheres, the third ventricle comes to form as it were the front end of the cerebrospinal axis, the crura cerebri expanding on each side of the third ventricle into the cerebral hemispheres which cover up the ventricle on the dorsal surface but leave its walls exposed on the ventral surface. Attached to the dorsal surface of the third ventricle at its hind end, ventral to and somewhat projecting beyond the base of the fornix, lies the pineal gland with its attachments, the remnants of a once-important median organ; and attached to the ventral surface of the ventricle, at the apex of a funnel-shaped projection, the infundibulum, lies the pituitary body, also a remnant of important ancestral structures.

§ **603**. We may then divide the whole brain into a series of parts corresponding to the main divisions of the embryonic brain. At the front lie the cerebral hemispheres, with the lateral ventricles, developed out of the cerebral vesicles; and with these are associated the corpora striata, the term cerebral hemisphere being sometimes used so as to include these bodies, and sometimes so as to exclude them. Next come, corresponding to the original fore-brain, the parts forming the walls of the third ventricle, conspicuous among which are the optic thalami; for these bodies though they appear to intrude into the lateral ventricles belong properly to the third ventricle. In the mid-brain which follows, the cavity, now the tubular passage of the aqueduct, is roofed in by the two pairs, anterior and posterior, of corpora quadrigemina, the dimensions of which are not very great; but a thick floor is furnished by the crura cerebri. In each crus we must distinguish between a dorsal portion called the *tegmentum*, in which a large quantity of grey matter is present and in which a great complexity in the arrangement of fibres exists, and a ventral portion, the *pes* or *crusta*, which is a much more uniform mass of longitudinally disposed fibres. As the crura passing forward diverge into the cerebral hemisphere on each side, the tegmentum ceases at the hinder end and ventral parts of the optic thalamus; it is the pes which supplies the mass of fibres radiating into each cerebral hemisphere. In a view of the ventral surface of the brain, the base of the brain as it is frequently called, the crura may be seen emerging from the anterior border of the pons. This we have spoken of as the thickened floor of the front part of the hind-brain, but in reality, it encroaches a little on the mid-brain, the hind part of the corpora quadrigemina being in the same dorsoventral plane as the front part of the pons (see Fig. 112). In the main, however, the pons belongs to the fore part of the hind-brain, the roof and sides of which are developed as we have said into the cerebellum. This superficially resembles the cerebral hemispheres in its large size, and in the special development of its surface, which is formed of grey matter folded in a remarkable manner and often spoken of as cortex. The cerebellum, though the lateral portions, called the hemispheres, project above the median portion, called the vermis, is, unlike the cerebrum, a single mass; each lateral half however sends down ventrally a mass of fibres which, running transversely, end in the pons; this mass of fibres, thus constituting as we have said a considerable part of the pons, forms on each side, just as it leaves the cerebellum to enter the pons, a thick strand, called the *middle peduncle* of the cerebellum. From the cerebellum there also proceeds backwards into the bulb on each side a thick strand of fibres, the *inferior peduncle* of the cerebellum or restiform body; and a third strand, the *superior peduncle* of the cerebellum, passes forwards on each side into the region ventral to the corpora quadrigemina. As the latter converge towards each other behind the corpora quadrigemina the angle between them is filled up by a thin sheet of nervous matter, the *valve of Vieussens*, which thus for a little distance backwards forms a roof for the front part of the fourth ventricle, just where the lozenge-shaped cavity is narrowing to become the aqueduct. Behind the cerebellum and pons comes the bulb, which as we have said is the thickened floor of the hind part of the hind brain, the roof of the cavity being here practically wanting.

Of these several divisions, the first division, that of the cerebral hemispheres, including the corpora striata, stands apart from the rest by reason both of its origin and the character of its development. As we shall see, this anatomical distinction corresponds to a physiological difference.

Of the other parts of the brain the crura cerebri deserve special attention. We may regard these as starting in the cord but largely augmented in the bulb; they traverse the pons, where they are still further increased, and passing beneath the corpora quadrigemina, with which as well as with the cerebellum they make connections, end partly in the region of the optic thalami and walls of the third ventricle, but to a great extent in the cerebral hemispheres. We may in a certain sense consider the rest of the brain as built upon and attached to these fundamental basal or ventral strands.

§ 604. Connected with the brain are a series of paired nerves, the cranial nerves. The first and second pair, the olfactory nerves and the optic nerves, differ in their origin and mode of development from all the rest so fundamentally as to cause regret that they are included in the same category. We shall consider these by themselves in due course. The remaining pairs, from the third pair to the twelfth, forming a much more homogeneous category, we shall also consider in their proper place. We must now turn to study in greater detail some of the structural features of the brain, and we may with advantage begin with the bulb.

SEC. 2. THE BULB.

§ **605**. The spinal cord, as it ascends to the brain, becomes changed into the more complex bulb, partly by a shifting of the course of the tracts of white fibres, partly by an opening up of the narrow central canal into the wide and superficial fourth ventricle, but chiefly by the development of new grey matter.

When the anterior, ventral, aspect of the bulb is examined (Fig. 112, C), it will be seen that the ventral columns of the cord are interrupted for some distance in the median line by bundles of fibres (*Py. dec.*) which, appearing to rise up from deeper parts, cross over from side to side and so confuse the line of the ventral fissure. This is the *decussation of the pyramids*, above which the place of the ventral columns of the spinal cord is taken by two larger, more prominent columns, the *pyramids* of the bulb (*Py.*), which are continued forwards to the hind margin of the pons. On the outer side of, lateral to, each pyramid, lies a projecting oval mass, *the olivary body* or *inferior olive* (*ol.*) separating the pyramid from a column of white matter, *the restiform body* (*R*), which, occupying the lateral region of the bulb, when traced backwards appears to continue the line of the lateral column of the cord, and when traced forwards is seen to run up to the cerebellum as the inferior peduncle of that organ. On the posterior, dorsal, aspect no such decussation is seen. The two dorsal columns of the cord diverge from each other, leaving between them a triangular space, the *calamus scriptorius*, which is the hind part of the lozenge-shaped shallow cavity of the fourth ventricle. As the cord passes into the bulb the dorsal column as a whole grows broader, and the division into a median posterior and an external posterior column becomes very obvious and distinct by the appearance of a conspicuous furrow separating the two. At some distance however in front of the point of divergence of the columns or apex of the calamus scriptorius, the furrow becomes less marked, and it eventually fades away. In its course the furrow takes such a line that the median posterior column, forming the immediate lateral boundary of the fourth ventricle,

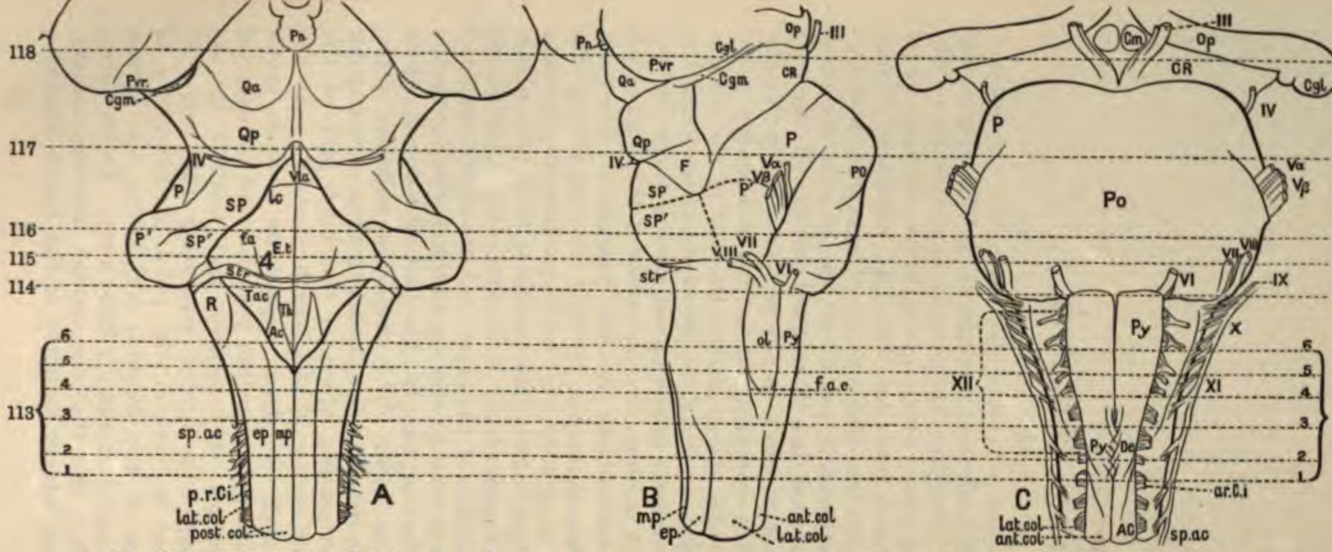


Fig. 112. Outlines of Parts of the Brain. A. Dorsal. B. Lateral. C. Ventral Aspect. (Nat. size.) (Sherrington.)

ant. col. ventral, *lat. col.* lateral, *post. col.* dorsal column of spinal cord. *m. p.* median posterior column (fasciculus gracilis). *e. p.* external posterior column (fasciculus cuneatus). *Py. de.* Decussation of pyramids. *Py.* pyramid. *ol.* olivary body. *A. c.* ala cinerea. *T. ac.* tuberculum acusticum. *str.* striæ acusticæ. *E. t.* eminentia teres. *F. a.* fovea anterior. *l. c.* locus cæruleus. *f. a. e.* external arcuate fibres. *Vla.* valve of Vieussens. *R.* restiform body. *Po.* pons. *S. P.* superior peduncle, *P.* part of middle peduncle of cerebellum, *SP'. P'.* the same two peduncles cut across; in *B* the limits of each are marked by dotted lines cut across. *CR.* crus cerebri. *Q. P.* posterior, *Q. A.* anterior corpus quadrigeminum. *F.* lateral fillet. *Op.* optic tract. *C. g. l.* lateral, *C. g. m.* median corpus geniculatum. *Pvr.* pulvinar of optic thalamus. *P. n.* pineal gland. *c. m.* corpora mammillaria or albicantia. *p. r. C.* 1. dorsal rootlets of IInd cervical nerve (in man the 1st cervical has rarely any dorsal rootlets), *a. r. C.* 1. ventral roots of the first cervical nerve. *sp. ac.* spinal roots of spinal accessory. XII. to III. cranial nerves. V. *α.* motor root, V. *β.* sensory root of fifth. 4. fourth ventricle.

The transverse lines indicate the levels of the sections in Figs. 113—118.

has the appearance of a strand broad behind but thinning away in front, while the external posterior column, also broadening as it advances forwards, seems to be wedged in between the median posterior column on its median edge and the restiform body on its lateral edge; hence the former is here called the *fasciculus* (or *funiculus*) *gracilis* (*m. p.*), and the latter the *fasciculus* (or *funiculus*) *cuneatus* (*e. p.*). Further forward both columns seem to merge with each other and with fibres which curve round to form part of the restiform body; the relations however of these two columns to each other and to the other parts of the bulb, as well as the nature of the other several changes by which the cord is transformed into the bulb, are disclosed by transverse vertical (dorso-ventral) sections, to the study of which we must now turn.

A section (Fig. 113, 1) taken at the hind margin of the decussation, at which level the first cervical nerve takes origin, when compared with a section of the cord at the level of the second cervical nerve (cf. Fig. 107, C_2), shews that certain changes are already taking place in the grey matter. The ventral horns are not much altered, but the dorsal horns are, as it were, pushed out laterally and dorsally so that the dorsal columns, which as yet retain their previous great depth, become very much broader than they are lower down, encroaching, so to speak, on the lateral columns. At the same time the substance of Rolando (*s. g.*), forming the head or caput of the horn, has enlarged into a more or less globular form, and lies near the surface of the cord though separated from it by a compact tract of longitudinal fibres (*V. a.*), which as we shall see, belongs to the fifth cranial nerve. A considerable development of the reticular formation (*f. ret.*) at the side of the grey matter ventral to the dorsal horn has also taken place, and this with the shifting of the position of the dorsal horn has driven the lateral horn (*l.h.*) nearer to the ventral horn. From this lateral horn a root of the eleventh spinal accessory cranial nerve (XI) may be seen taking origin. Further, a great increase of grey matter round the central canal may also be observed.

These changes, however, are of degree only; what seems to be an absolutely new feature is the presence of bundles of fibres (*Py. dec.*), which starting from the ventral column of one side cross over to and are apparently lost in the grey matter of the neck of the ventral horn of the other side; in so crossing the fibres push aside the bottom of the ventral fissure. When the course of these fibres is investigated, either by simple microscopic observation, or still better by the method of degeneration, it is found that they may be traced from the ventral column of one side, across the ventral commissure, through the neck of the ventral horn to the lateral column of the opposite side, and to that part of the lateral column which we have previously described as the crossed pyramidal tract.

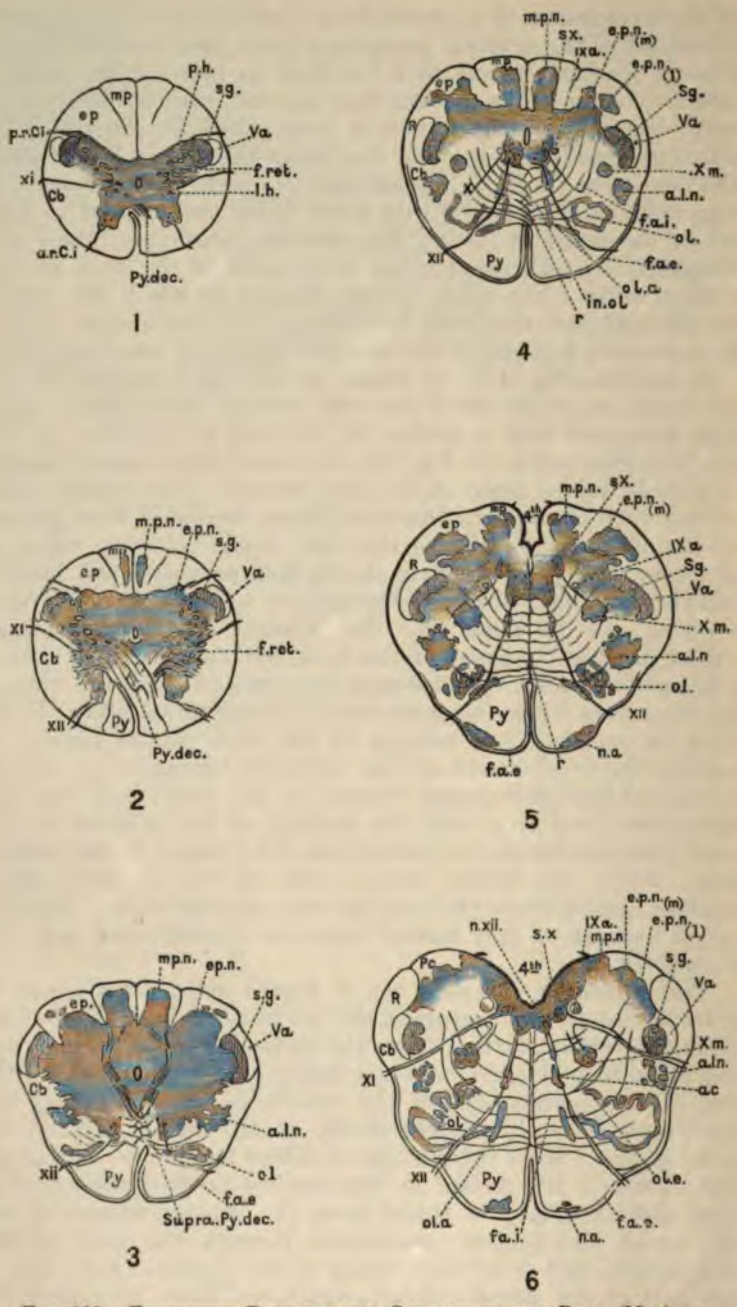


Fig. 113. Transverse Dorsoventral Sections of the Bulb (Man) at Different Levels. (Sherrington.)

This and Figs. 114—118, form a series of transverse dorsoventral sections of the brain taken at different levels from the hind end of the bulb to the front of the third ventricle; the several levels are shewn by the lines drawn in Fig. 112. They are all magnified twice. The details are shewn, for the sake of simplicity, in diagrammatic fashion; the white matter is left unshaded, the course of the fibres being indicated in a few important instances only; the grey matter is shaded formally, the nerve-cells being indicated in the case only of the nuclei of the cranial nerves. The want of complete bilateral symmetry which is often met with in such sections is indicated in several of the figures.

1. At the hind limit of the decussation of the pyramids. 2. In the middle of the decussation. 3. At the upper end of the decussation. 4. Just below the point of the calamus scriptorius. 5. Just above the point. 6. Through the middle of the ala cinerea.

Py. Pyramids. *Py. dec.* decussation of the pyramids. *Supra Py. dec.* superior decussation. *f. a. i.* internal arcuate fibres. *f. a. e.* external arcuate fibres. *Cb.* position of cerebellar tract. *R.* restiform body or inferior peduncle of the cerebellum. *e. p.* external posterior column, fasciculus cuneatus, *m. p.* median posterior column, fasciculus gracilis. *r.* raphe.

l. h. lateral horn. *m. p. n.* nucleus of the median posterior column or gracile nucleus. *e. p. n.* nucleus of the external posterior column or cuneate nucleus. *e. p. n.* (*m.*) median division and *e. p. n.* (*l.*) lateral division of the same. *ol.* olivary body. *ol. a.* median accessory, and *ol. e.* lateral accessory olive. *in. ol.* interolivary layer. *a. l. n.* lateral (antero-lateral) nucleus. *n. a.* arcuate nucleus. *a. c.* remnant of ventral horn. *f. ret.* reticular formation. *s. g.* substance of Rolando.

a. r. c. I. ventral root, and *p. r. c.* II. dorsal root of second cervical nerve. XI. root of spinal accessory nerve. XII. twelfth or hypoglossal nerve. *n.* XII. nucleus of the same in 6; the nucleus may be traced however through 2, 3, 4, 5, in connection with the fibres of the nerve. *s.* X. sensory or main part of the glossopharyngeal-vago-accessory nucleus. X. *m.* motor nucleus of the vagus, or nucleus ambiguus. IX. *a.* ascending root of the glossopharyngeal nucleus. V. *a.* ascending root of the fifth nerve.

4th. fourth ventricle; the ependyma or lining is indicated by a thick dark line; and in 5 and 6, the tooth-like section of the projecting obex is shewn.

In a section a little higher up (Fig. 113, 2), these decussating fibres form on each side a large strand which starts from a part of the ventral column, now becoming distinctly marked off as the pyramid (*Py.*), and is apparently lost in the reticular formation, but in reality passes on to the crossed pyramidal tract of the lateral column. This strand, as it crosses over, completely cuts off the head of the ventral horn from the more central grey matter, and forms with its fellow a large area of decussating fibres between the bottom of the ventral fissure and the central grey matter. When a surface view of the bulb is examined the decussation is seen to be effected by alternate bundles, passing now from right to left, now from left to right; and in transverse sections we find correspondingly that the ventral fissure appears bent now to the left and now to the right, according as the section cuts through a bundle passing from left to right or from right to left.

In sections still higher up (Fig. 113, 3 and 4) this conspicuous strand of fibres crossing obliquely from side to side, will be no longer seen; decussating fibres are seen dorsal to the ventral fissure, but these, of which we shall speak presently, are of different nature and origin. The fibres which in sections below were seen in the act of crossing are now gathered into masses of longitudinal fibres, the pyramids, (*Py.*) one on each side of the ventral fissure, each with a sectional area of a rounded triangular form clearly marked out from the surrounding structures; the section is taken above the decussation of the pyramids. Or, tracing the changes from below upwards we may say that the decussation is now complete; on each side the whole of the crossed pyramidal tract of the spinal cord has, in the region of the bulb below the level of the present sections, crossed over to the other side, and joining with the direct pyramidal tract of the ventral column of the cord of the same side has become the pyramid of the bulb. In other words, the decussation of the pyramids is, as we have already hinted, the passing off from each pyramid, and the crossing over to the opposite side of the cord, of those fibres which are destined to become the crossed pyramidal tract of the spinal cord of the opposite side, while the rest of the pyramid pursues its course on the same side partly as the direct pyramidal tract of the ventral column and partly as fibres in the lateral column scattered among the fibres of the crossed pyramidal tract in that column.

§ **606**. In the spinal cord the bottom of the ventral fissure is separated from the central canal by nothing more than the ventral white commissure and a narrow band of grey matter, composed of the ventral grey commissure and of part of the central gelatinous substance. During the decussation of the pyramids, the decussating fibres push, as it were, the central canal with its surrounding grey matter to some distance from the bottom of the ventral fissure. In sections above the decussation the bottom of the fissure does not again approach the central canal, but continues to be removed to some distance from it, and, as we pass upwards, to an increasing distance, by the interposition of tissue which consists largely of decussating fibres. These however, though they seem to continue on the decussation of the pyramids, are shewn by the embryological and degeneration methods to have no connection with the pyramids, but to belong to another system of decussation. As we have seen (§ 565) the ventral white commissure along the whole length of the cord contains decussating fibres. Some of these in the upper part of the cord are fibres crossing from the direct pyramidal tract of one side to the grey matter of the other side, and so may be regarded as part of the whole pyramidal tract; but others are of different origin; and even in the region of the actual decussation of the pyramids some of the fibres which cross over do not belong to the pyramidal tract. This system of decussating fibres becomes increasingly prominent above the decussation of the pyramids, and through it the ventral area of the bulb between the central canal and the ventral fissure is much increased. The fibres as they cross form a middle line of partition, the *raphe* (Fig. 113, 4, 5, *r*), which increases in depth in the upper parts of the bulb, and on each side of the raphe help to break up the grey matter (which previously formed the ventral horns) into what is called the *reticular formation*. We shall return to this presently, but may here call attention to a special development of these decussating fibres which is seen just above the decussation of the pyramids. In a section at this level (Fig. 113, 3) a strand of fibres (*supra Py. dec.*) may be seen to start chiefly from the gracile nucleus but also to some extent from the cuneate nucleus, to sweep round the central grey matter, and to decussate ventral to this between it and the bottom of the ventral fissure. This is called the *superior decussation*, or, for reasons which we shall see later on, the *sensory decussation*.

§ **607**. We must now turn to the dorsal fissure and its relations to the fourth ventricle. We saw that at the beginning of the pyramidal decussation, the dorsal horns had been thrown backwards and outwards so as to increase the dorsal columns. The dorsal fissure is still of great depth, so that by the increase of breadth and maintenance of depth the dorsal column, the lateral limit of which is still sharply marked out by the swollen head of the dorsal horn as well as by the highest dorsal rootlets of the second cervical nerve, acquires at this level its maximum of bulk.

From this point forward the depth of the dorsal fissure and the dorso-ventral diameter of the dorsal columns diminishes. The head of the horn (Fig. 113, 2) is thrown still further outwards into the lateral regions; developments of grey matter at the base and to some extent at the neck of the horn (of these we shall speak presently) encroach (Fig. 113, 3) dorsally on the white matter of the columns; and the central grey matter appears to rise dorsally at the expense of the dorsal fissure, in coincidence with the development described above as taking place on the ventral side of the canal.

Still a little further forward, in a section for instance (Fig. 113, 4) a little way behind the apex of the *calamus scriptorius*, the central grey matter, which still forms a rounded mass around the central canal, is brought yet nearer to the dorsal fissure.

In a section yet a little further forward (Fig. 113, 5) carried through the hinder narrow part of the fourth ventricle itself, it is seen that the central canal has opened out on to the dorsal surface, and that the grey matter, which in previous sections surrounded it, is now exposed to the surface on the floor of the ventricle, the median posterior columns being thrust aside. In a still more forward section (Fig. 113, 6) this grey matter in correspondence with the increasing width of the ventricle occupies a still wider area, thrusting still further aside the narrowing upper ends of the two posterior columns.

During these successive changes, the large wide dorsal (both external posterior and median posterior) columns of the cervical spinal cord and beginning bulb, are reduced to small dimensions and in the end disappear; but before we speak of the course and fate of the tracts of fibres constituting these columns we must turn to the important changes of the grey matter.

§ **608**. A transverse section through the lower end of the decussation (Fig. 113, 1) shews, as we have said, few differences as regards the grey matter from one taken at the level of the second cervical nerve. The changes noticeable are mainly the changes in position of the dorsal horns, the increase of central grey matter around the central canal, the approach of the lateral horn, from which spring the roots of the spinal accessory nerve, to the ventral horn, and an increase of the reticular formation in the bay ventral to the dorsal horn.

In the middle of the decussation (Fig. 113, 2) the decussating fibres are cutting the head of the ventral horn away from the base of the horn and the central grey substance, and the isolated head is diminishing in size, being separated from the surface of the cord by an increasing thickness of white matter. The lateral horn and origin of the spinal accessory root do not share in this isolation, but are driven back again dorsally towards the dorsal root to join the reticular formation which is increasing in area, while the lateral column of white matter is diminishing in bulk by the withdrawal of the pyramidal tract.

Still a little further forward, the ventral horn seems at first sight to have wholly disappeared (Fig. 113, 3 and 4), but its disappearance is coincident with an increase of the reticular formation in the position of the lateral columns, as well as with the growth of tissue mentioned above between the ventral fissure and the central grey matter. In fact, between the pyramids on the ventral side and the largely increased and laterally expanded grey matter on the dorsal side, a large area of peculiar tissue now extends on each side for a considerable distance from the middle line of the raphe, encroaching on what was the lateral column of white matter; and a corresponding area of similar tissue may be traced from this level through the higher parts of the bulb up into the pons and crura cerebri. The tissue consists of nerve fibres running transversely, longitudinally, and in other directions, so as to form a network, the bars of which are often curved; and with these fibres are found branched nerve cells in considerable number, some of them small, both fibres and cells being as elsewhere embedded in neuroglia. Though differing from the ordinary grey matter of the cord by the more open character of its network, it may be considered as a form of grey matter. We may consider it as being in reality the grey matter of the apparently lost ventral horn broken up and dispersed by the passage of a large number of fibres and bundles of fibres, especially of the decussating fibres spoken of in § 606, which since they curve through this area from the middle line laterally are called arcuate or arciform fibres, *internal arcuate fibres* (Fig. 113, 6, *f. a. i.*) to distinguish them from the *external arcuate fibres* (*f. a. e.*) of which we shall speak presently. Fragments of more compact grey matter, also belonging probably to the ventral horn, are seen at intervals in this area, Fig. 113, 6, *ac.* and elsewhere. We have seen that nearly all the way along the cord the grey matter of the neck of the dorsal horn is similarly broken up by bundles of fibres into what we there called the reticular formation (Figs. 99, 100, *r. f. p.* and *r. f. l.*); and this area in the bulb though it possesses characters of its own is also called *the reticular formation.* In the more lateral portion of this formation, the network is more open and irregular, the bars are finer, and the nerve cells are more abundant than in the median portion where the nerve cells, except in the immediate neighbourhood of the raphe, are less numerous or even absent, and the bars are coarser. These two parts are sometimes distinguished as the grey or lateral, and the white or median formation. In the middle line the fibres distinctly interlace and decussate in an oblique manner, some running nearly vertically in the dorsoventral plane, thus constituting as we have said a thick raphe, which, however, at its edges gradually merges into the more open network.

§ **609**. Within the area, bounded by the pyramids ventrally, the expanded grey matter dorsally, the raphe in the middle line, and the white matter laterally, certain distinct compact masses of grey matter make their appearance, as we pass upward towards the pons.

One of the most important of these gives rise to the *olivary body,* or *inferior olive* which, as we have seen, projects as an oval mass (Fig. 112, *ol.*) on each side of the pyramids, reaching from a level which is somewhat higher up than the lower limit of the pyramids, almost but not quite to the pons. The olivary body, as a whole, consists partly of white matter, that is of fibres, and partly of grey matter, sometimes called the *olivary nucleus.* This latter is disposed in the form of a hollow flask or curved bowl, with deeply folded or plaited walls, having a wide open mouth directed inwards towards the middle line, and forwards towards the pons (Fig. 113, 4, 5, 6, *ol.*). The flask is filled within by white matter, and covered up on its outside with white matter as well as traversed by fibres. The grey matter thus forming this flask-shaped nucleus consists of small rounded nerve cells, lying in a bed of tissue which is partly ordinary neuroglia, and partly a fine nervous network.

Lying to the median side of the olivary body, immediately dorsal to the pyramid, is another small mass of grey matter, in the form of a disc, appearing in transverse sections as a thick bent rod, in some sections consisting of two parts (Fig. 113, 4, *ol. a*).

This is the *accessory olivary nucleus.* A very similar body lies dorsal to the olivary nucleus, in the lateral reticular formation; this is also called an accessory olivary nucleus, being distinguished (Fig. 113, 6, *ol. e*) by the name *outer accessory* nucleus from the above-mentioned *inner accessory* nucleus. It will be observed in these transverse sections that the inner accessory nucleus is separated from the olivary nucleus by a bundle of white fibres (Fig. 113, 4, 5, 6, XII) which, running ventrally from the grey matter in the dorsal region, comes to the surface between the pyramids and the olivary body. This is the hypoglossal or twelfth cranial nerve.

On the surface of the pyramid itself is seen on each side a small mass of grey matter (Fig. 113, 5, 6, *n. a.*), which since it appears to be connected with a system of superficial transverse fibres, which we shall describe directly as the *external arcuate fibres* (Fig. 113, 3, 4, 5, 6, *f. a. e.*), is called the *arcuate nucleus.*

Lastly, a small somewhat diffuse collection of grey matter is seen in sections as a rounded mass of irregular form placed lateral to the reticular formation (Fig. 113, 4, 5, 6, *a. l. n*). This, which at its first appearance seems to be budded off from the general mass of grey matter (Fig. 113, 3, *a. l. n*), and which is probably a detached portion of the base of the ventral horn or of the lateral region of the grey matter, is called the *lateral* or *antero-lateral* nucleus.

Hence, besides the diffuse reticular formation, this ventral part of the bulb contains more sharply defined collections of grey matter in the olivary nucleus, and the other bodies just mentioned.

§ 610. We must now turn to the dorsal part of the bulb. Here in the first place we must distinguish between the portions of grey matter which are more immediately connected with the cranial nerves taking origin from this part of the bulb, and the portions which have no such obvious connection. In the spinal cord, the ventral horns supply, as we have seen, the origins of the successive ventral motor nerves; but in the transformation of the cord into the bulb the ventral horns have been broken up or displaced; and the parts of the ventral horns, serving as the nuclei of origin for motor nerves, have been translated from the ventral to the more dorsal regions. Hence, it is in the more dorsal part of the grey matter that we have to seek for the nuclei of origin not only of afferent but also of motor cranial nerves. It will be convenient to consider all these nuclei of origin of cranial nerves by themselves, and we may here confine ourselves to the grey matter of other nature. We may however say that these nuclei, or nearly all of them, from that of the third nerve backwards are more or less closely associated with the grey matter immediately surrounding the central canal. This *central grey matter*, in the narrow sense of the term, is marked out somewhat low down (Fig. 113, 3) by the fibres of the sensory decussation which sweep round it; it appears in sections higher up as a fairly distinct region (Fig. 113, 4); and it is this part of the grey matter which is exposed on the floor of the fourth ventricle when the central canal (Fig. 113, 5, 6) opens out into that space. We say exposed; but in reality the true grey matter is covered by a superficial layer of tissue of a peculiar nature (indicated in Fig. 113, 5, 6, by a thick black line) similar to that which is found at the hind end of the conus medullaris in the spinal cord.

We saw that at the level of the first cervical nerve coincident with the horizontal flattening out of the posterior horns the dorsal columns assumed very large dimensions. In this region (Fig. 113, 1) they consist entirely of white matter, that is, of longitudinal fibres.

At a little higher level, however, at the level of the middle of the decussation for example, an islet of grey matter (Fig. 113, 2, *m. p. n.*) makes its appearance in the median posterior column. A little further forward, at the level of the established pyramids, it will be seen (Fig. 113, 3) that this islet is the hind end of an invasion from the more centrally placed grey matter, and that at the same time there has taken place a similar inroad of grey matter into the external posterior column (Fig. 113, 3, *e. p. n.*); indeed a slight extension of grey matter into the external posterior column may be seen even before this (Fig. 113, 2, *e. p. n.*). It will further be observed that these grey masses have so largely encroached on the white matter, that both the median posterior or fasciculus gracilis and the external posterior column or fasciculus cuneatus, instead of being simply tracts of white fibres as they were in the hinder part of the bulb and in the cord, have now become columns of grey matter covered by a relatively thin layer of white fibres. These columns of grey matter are now called respectively the *median posterior nucleus,* or *nucleus fasciculi gracilis,* or more shortly, the *gracile nucleus;* and the *external posterior nucleus,* or *nucleus fasciculi cuneati,* or the *cuneate nucleus.* From the ventral aspect of these nuclei a large number of fibres pass ventrally with a more or less curved course to form as we have seen, § 606, the superior decussation and to pursue certain paths through the reticular formation, of which we shall speak later on. It is at this level and for some little distance above (Fig. 113, 4, 5), that these nuclei acquire their greatest development. Farther forward (Fig. 113, 6), when the fourth ventricle has opened out and the nuclei of the cranial nerves are becoming conspicuous, and the posterior columns have been thrust aside laterally, both these nuclei have diminished in size; still farther forward they become still smaller, and towards the pons they gradually disappear.

The mass of gelatinous substance, forming at the level of the first cervical nerve the swollen caput of the horn close to the surface but separated from it by a band of fibres (*Va*) of fine calibre, to which we have already referred as belonging to the fifth cranial nerve, increases in bulk at a somewhat higher level, Fig. 113, 2, 3, *s.g.*, and forms on the surface a slight projection, called *the tubercle of Rolando*. It soon, however, becomes thrust ventrally by the divergence of the dorsal columns, and more and more covered up by the fibres which are going to form the increasing restiform body, Fig. 113, 4, 5, 6, *R*. Retaining this position the islet of gelatinous substance diminishes in size farther forwards, Fig. 114, *s.g.*, and eventually disappears.

§ **611**. *The Fibres of the Bulb.* It is obvious, from what has already been said, that the arrangement into dorsal, lateral and ventral columns, so clear and definite in the spinal cord, becomes broken up in the bulb: indeed it will be best in treating of the bulb, not to attempt to trace out these columns, but to speak of the course of the several tracts into which these columns may be divided.

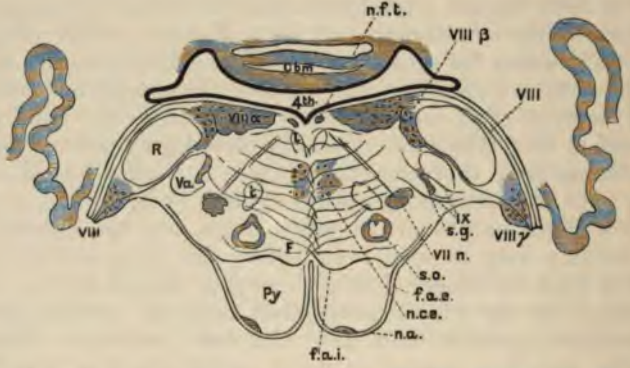


Fig. 114. Through the Bulb just behind the Pons. (Sherrington.)
Taken in the line 114, Fig. 112.

Py. Pyramids. *R*. Restiform Body. *Cbm*. cerebellum. *F*. Fillet. *f. a. e.* external, *f. a. i.* internal arcuate fibres. *t*. bundle of fibres from olive to the lenticular nucleus. *l*. posterior longitudinal bundles. *n. f. t.* nucleus of fasciculus teres. *s. o.* superior olive. *n. c. e.* nucleus centralis (the marks within it are sections of bundles of fibres by which it is traversed). *s. g.* substance of Rolando.

V. *a*. ascending root of fifth nerve. VII. *n*. nucleus of the 7th nerve. VIII. auditory nerve, chiefly the dorsal or cochlear root; VIII. α. median nucleus, VIII. β. lateral nucleus, VIII. γ. accessory nucleus of auditory nerve. IX. fibres of root of ninth nerve passing through ascending root of fifth nerve.

The direct and crossed pyramidal tracts of the cord unite to form, as we have seen, the pyramid of the bulb, and so pass on to the pons. We need say nothing more at present concerning this important pyramidal strand except that, as we trace it down from the pons to the spinal cord, it gives off to the bulb itself fibres which make connections with the motor fibres of the cranial nerves proceeding from this region.

Concerning the course taken by the other less conspicuous "descending" tract, the antero-lateral descending tract, our knowledge is very imperfect; nothing definite can be said at present.

The cerebellar tract, occupying near to the surface a position which in the series of sections (Fig. 113, *Cb*) appears now rather more ventral, now more dorsal, eventually passes into the restiform body, of which it forms a large part, and thus reaches the cerebellum. The antero-lateral ascending tract does not take this course; its fibres are continued forward beyond the bulb into the pons, though they, or some of them, reach the cerebellum thence in a roundabout way by the superior peduncle.

The median posterior tract or column, becoming the fasciculus gracilis, ends in the gracile nucleus; and in a similar manner the external posterior column, or fasciculus cuneatus, ends in the median and lateral masses of the cuneate nucleus. As we have seen, the white matter of these columns diminishes as the nuclei increase; and the nuclei after absorbing, so to speak, the white matter diminish in turn; the ascending degeneration observed in these columns stops at these nuclei.

The remaining fibres of the cord, belonging partly to the ventral column and partly to the lateral column, not gathered into any of the above-mentioned tracts, appear to end chiefly at all events in the reticular formation of the bulb itself, though some are carried on to the higher parts of the brain.

§ **612**. Thus of the various tracts or strands of the spinal cord two only pass as conspicuous unbroken strands through the bulb to or from higher parts; namely, the pyramidal tract to the cerebrum and the cerebellar tract to the cerebellum. With the further exception of the fibres of the antero-lateral ascending tract, all or nearly all the rest of the longitudinal fibres of the cord reaching the bulb end, as far as we know at present, in some part or other of the bulb; and we may infer that some or other nerve cells of the bulb serve as relays to connect these fibres of the cord with other parts of the brain.

The gracile and cuneate nuclei stand out conspicuously as relays of this kind, and through them the dorsal columns of the cord make secondary connections on the one hand with the cerebellum and on the other hand with various regions of the cerebrum. We have said § 606 that fibres passing ventrally from the gracile and cuneate nuclei sweep in a curved course through the reticular formation as the internal arcuate fibres (Fig. 113, *f. a. i.*). The hindmost of these form the superior decussation already referred to as seen in sections at the fore-part of and in front of the pyramidal decussation (Fig. 113, 3, *supra Py. dec.*). After decussating ventral to the central canal these fibres form an area called the *inter-olivary layer* (Fig. 113, 4, *in. ol.*) lying dorsal to the pyramids between the two olivary nuclei. This layer may be regarded as the hind end or beginning on each side of a remarkable longitudinal strand called the *fillet* (Figs. 112, *B.F.*, 114, *F.*), of the connections of which in the front part of the brain we shall speak hereafter. Thus these two nuclei are the source of fibres which cross to the other side of the bulb, and reaching the inter-olivary layer dorsal to the pyramids run up to higher parts of the brain by the fillet.

The gracile and cuneate nuclei give rise also to other fibres which, though also sweeping ventrally and crossing to the other side, do not, when they reach the inter-olivary region, assume a longitudinal direction as do the fibres forming the fillet, but as external arcuate fibres (Fig. 113, *f. a. e.*) pursue a course which is at first ventral along the side of the anterior fissure and then lateral over the ventral surface of the pyramid and olivary nucleus, by which path they reach the lateral surface of the bulb, and so the restiform body and cerebellum. In this way, the two nuclei in question contribute to the restiform body of the opposite side of the bulb. These external arcuate fibres, which as they sweep round the ventral surface of the pyramid traverse the arcuate nucleus, though they vary much in individual brains, form a considerable portion of the white matter seen on the ventral and lateral surfaces of the bulb; it is by them that the olivary nucleus is covered up.

The cuneate and gracile nuclei, besides this crossed and somewhat roundabout connection with the restiform body of the opposite side, have also a direct connection with the restiform body of the same side; fibres pass by a more or less direct lateral path from them to it. Thus the two nuclei are connected with the opposite side of the cerebellum by external arcuate fibres, and with the same side of the cerebellum by the other fibres just mentioned. The connection between the two nuclei and the cerebellum is large and important; and as the nuclei diminish forwards the restiform body increases in bulk.

Hence the important strand of fibres which is called in the bulb the restiform body, and higher up the inferior peduncle of the cerebellum, is connected with the spinal cord in two chief ways: directly by means of the cerebellar tract, and indirectly by means of the cuneate and gracile nuclei. By the relay of the gracile nucleus it is brought into connection with the median posterior column along the whole length of the cord, and so with that division of the dorsal roots which (§ 577) in the several spinal nerves goes to form that column. By the relay of the cuneate nucleus it is brought into connection with such parts of the external posterior column as end in that nucleus, and thus probably with other fibres of the dorsal roots of the upper spinal nerves. And if we admit that the cerebellar tract is connected, by the relay of the vesicular cylinder or by other nerve cells, with the rest of the dorsal roots of the spinal nerves, we may conclude that the restiform body is, by means of these relays, a prominent continuation of all the spinal dorsal roots.

The restiform body and so the cerebellum is also specially connected with the olivary body of the opposite side; for when in young animals one side of the cerebellum is removed the olivary body of the opposite side atrophies. The fibres maintaining this connection appear to pass from the olivary nucleus of one side through the interolivary layer and thence laterally through the reticular formation of the other side to the restiform body and so to the cerebellum. Lastly we may add that a tract which is sometimes included in the restiform body as its median or inner division has quite a different origin from any of the above; the fibres which compose it come, as we shall see, from the auditory nerve.

The further connections of the bulb with the cerebrum it will be best to leave until we come to deal with the structural arrangement of the rest of the brain.

Meanwhile enough has been said to shew that the bulb differs very materially in structure from the spinal cord. The grey matter of the bulb is far more complex in its nature than is that of any part of the cord; and the arrangement of the several strands and tracts of fibres is far more intricate. The structural features on the whole perhaps suggest that the main functions of the bulb are twofold; on the one hand it seems fitted to serve as a head centre governing the spinal cord, the various reins of which, with the exceptions noted, it holds as it were in its hands; on the other hand it appears no less adapted to act as a middleman between parts of the spinal cord below and various regions of the brain above. As we shall see experiment and observation give support to these suggestions.

SEC. 3. THE DISPOSITION AND CONNECTIONS OF THE GREY AND WHITE MATTER OF THE BRAIN.

The Grey Matter.

§ **613**. As we pass up from the bulb to the higher parts of the brain, the differentiation of the grey matter into more or less separate masses, which we have seen begin in the bulb, becomes still more striking. We have to distinguish a large number of areas or collections of grey matter more or less regular in form and more or less sharply defined from the surrounding white matter; to such collections the several terms corpus, locus, nucleus and the like have from time to time been given. These areas or collections vary greatly in size, in form and in histological characters; they differ from each other in the form, size, features and arrangement of the nerve cells, in the characters of the nervous network of which the nerve cells form a part, and especially perhaps in the extent to which the more distinctly grey matter is traversed and broken up by bundles of white fibres. Guided by the analogy of the spinal cord, as well as by the results of experiments and observations directed to the brain itself, we are led to believe that the complex functions of the brain are intimately associated with this grey matter; and a full knowledge of the working of the brain will carry with it a knowledge of the nature and meaning of the intricate arrangement of the cerebral grey matter. At present, however, our ignorance as to these things is great; and, though various theoretical classifications of the several collections of grey matter have been proposed, it will perhaps be wisest to content ourselves here with a very broad and simple arrangement. We will divide the whole grey matter of the brain into four categories only. 1. The central grey matter lining the neural canal; and with this we may consider the nuclei of the cranial nerves, some of which are closely associated with it. 2. The superficial grey matter of the roof of some of the main divisions of the brain, such as that of the cerebral hemispheres, and of the cerebellum. 3. The intermediate grey matter more or less closely connected with the crura cerebri. 4. Other collections and areas of grey matter. We will, moreover, confine ourselves at present for the most part to their general features and topography, reserving what we have to say concerning their histological characters for another occasion.

1. *The Central Grey Matter, and the Nuclei of the Cranial Nerves.*

§ **614**. The ventricles of the brain like the central canal of the spinal cord, of which they are a continuation, are lined by an epithelium which is in general a single layer of columnar cells said to be ciliated throughout, though it is often difficult to demonstrate the cilia. Beneath this epithelium lies a layer of somewhat peculiar neuroglia, forming with the epithelium, as we have said (§ 610), the *ependyma*, which, well developed in the floor of the fourth ventricle and in the walls of the third ventricle, and of the aqueduct, is thin and scanty in the lateral ventricles. Beneath, and more or less connected with the ependyma in the sides and floor of the third ventricle, is a fairly conspicuous layer of grey matter, which is well-developed in the parts of the floor exposed on the ventral surface of the brain, and known as the lamina terminalis, the anterior and posterior perforated spaces, the tuber cinereum &c. This layer is not continued forwards into the lateral ventricles of the cerebral hemispheres, but it is well-developed backwards along the aqueduct (Figs. 117, 118) and in the floor of the fourth ventricle, and through the bulb becomes, as we have seen (§ 610), continuous with the central grey matter of the cord. The nerve-cells of this grey matter are on the whole small and in many places scant.

§ **615**. The several roots of the cranial nerves from the third nerve backwards may be traced within the brain substance to special collections of grey matter, called the *nuclei of the cranial nerves*, some of which lie close upon the central grey matter, while others are placed at some distance from it. The optic nerve and what is sometimes called the olfactory nerve, namely, the olfactory bulb and tract, may advantageously be dealt with apart, since these two nerves are not, like the other cranial nerves, simple outgrowths from the walls of the original neural canal, but are in reality elongated vesicles, budded off from the neural canal, the cavities of which have been obliterated. We may add that part of the retina, and of the grey matter of the olfactory tract, may perhaps be considered as corresponding to the nuclei of which we are speaking, the retinal and proper olfactory fibres being connected with them very much as the fibres of the remaining cranial nerves are connected with their respective nuclei.

In the brain, the segmental regularity of the nerve roots so conspicuous in the spinal cord is very greatly obscured. We shall have something to say on this point later on; but at present we may be content to treat the several nerves in a simple topographical manner. They may be seen in a ventral view of the brain Fig. 112, C, leaving the brain at various levels by what is called their "superficial origin;" the third nerve issuing in front of the pons, and the last or hypoglossal stretching back to the hind end of the bulb. Part, indeed, of the eleventh nerve, the spinal accessory nerve properly so called, makes connections with the spinal cord below the bulb as far back as the sixth or seventh cervical nerve, or even lower; but this part may by these connections be distinguished from the remaining part of the nerve, as well as from all the other cranial nerves. The nuclei to which the nerve-roots may be traced within the brain substance, sometimes spoken of as the "real origin," range in position from the hinder part of the bulb to the hind end of the third ventricle. The nucleus of the hypoglossal nerve begins in the bulb just above the decussation of the pyramids, the nucleus of the third nerve ends beneath the hind end of the floor of the third ventricle; and all the rest of the nuclei may be broadly described as placed between these limits in various parts of the floor of the central canal or in adjoining structures, though part of one nucleus, namely, that of the fifth nerve, can be traced, as we shall see, back into the spinal cord as far as the second cervical nerve and probably extends still farther. Fig. 119 is a diagram shewing in a roughly approximate manner the nuclei of the several nerves as they would appear in a bird's-eye view of the floor of the aqueduct and fourth ventricle looked at on the dorsal aspect.

§ 616. *The Twelfth or Hypoglossal Nerve.* The nucleus of this nerve, which it will be convenient to take first (Fig. 119, XII.), is a long column of grey matter lying in the bulb parallel to, and very close to, the median line. It reaches from the hinder part of the fourth ventricle, at about the level of the hind end of the auditory nucleus, as far back as beyond the hind end of the olivary body. At its extreme hind end or beginning (Fig. 113, 2), it occupies a ventral position and is a part of the ventral horn; thence it gradually rises dorsally (Fig. 113, 3, 4, 5), but so long as the central canal remains closed continues to occupy a distinctly ventral position in reference to the central canal; in its front part, it is, by the opening up of the fourth ventricle, brought into an apparently more dorsal position (Fig. 113, 6).

The nucleus consists mainly of large nerve-cells with distinct axons, which though pursuing a somewhat irregular course may be traced into the fibres of the nerve. These, starting from the ventral surface of the nucleus along its length, run ventrally through the reticular formation, and making their way in a series of bundles, between the olivary nucleus on the lateral side and the pyramid and median accessory olive on the median side gain the surface along the groove which separates the pyramid from the olivary body.

§ **617**. *The Ninth or Glossopharyngeal, Tenth or Vagus,* and *Eleventh or Spinal accessory Nerves.* It will be advantageous to consider these three nerves together.

In the spinal accessory nerve we must distinguish, as we have said, two parts: the "spinal accessory" proper, formed by the roots which come off from the cervical spinal cord, reaching as far down as the sixth or seventh cervical nerve, and the "bulbar accessory," whose roots come off from the bulb just below the vagus.

The spinal accessory proper takes origin in the group of cells lying in the extreme lateral margin of the ventral horn, from whence the fibres proceed either directly or, after a short course in the grey matter, outwards through the lateral column, and issue from the cord along a line intermediate between the ventral and dorsal roots; the upper roots undergo, with the portion of the lateral horn from which they spring, the shifting spoken of in § 605.

The bulbar accessory may be traced to an elongated nucleus in the bulb which is common to it, to the vagus, and to the glossopharyngeal; hence we have taken these three nerves together. This (Fig. 119) stretches farther forward than the hypoglossal nucleus, reaching the level of the transverse fibres called striæ acusticæ (*str.*), but does not extend so far behind.

In transverse sections of the bulb, which pass a little below or a little above the point of the calamus scriptorius (Fig. 113, 4, 5), two nuclei or collections of cells are seen in the grey matter round the central canal. The more ventral one is the hypoglossal nucleus, the more dorsal one the beginning or hind part of the combined accessory-vago-glossopharyngeal nucleus.

When a little farther forward the central canal opens out into the fourth ventricle (by which change the hypoglossal nucleus (Fig. 109, 6 *n.* XII.) is brought nearer to the dorsal surface in the floor of the fourth ventricle) this combined nucleus, increasing in breadth, is thrown to the side and assumes a more lateral position, lying now on the side of, but still somewhat dorsal to, the hypoglossal nucleus, between it and the now diminishing gracile nucleus. In this position the nucleus appears to consist of two parts, a median and lateral, the median part having conspicuous nerve-cells of moderate size, the lateral part having but few cells, and those of small size. From this level the nucleus runs forwards, maintaining nearly the same position in the floor of the fourth ventricle but gradually becoming thinner, and ends as we have said at about the level of the striæ acusticæ on the dorsal surface corresponding on the ventral surface to a level a little behind the hind margin of the pons.

From this combined nucleus, but chiefly from the median part, fibres may be traced which sweeping in a ventral and lateral direction through the dorsal part of the reticular formation, pass ventral to, or in some cases through the gelatinous substance and the strand of fibres connected with the fifth nerve (Fig. 113, V. *a*), and reach the surface of the bulb on its lateral aspect in a line between the olivary and restiform bodies (Fig. 112, C). Along this line may be seen (Fig. 112, C) a series of roots; of these the lowest, the accessory roots, are connected with the hind part, the highest, the glossopharyngeal roots, with the front part (and it is these especially which pierce the gelatinous substance (Fig. 114, IX. *a*)), and the intermediate, the vagus roots, with the middle part of the combined nucleus. Hence we may speak of the hind part of the whole nucleus as being the accessory nucleus, the middle part as the vagus nucleus, and the front part as the glossopharyngeal nucleus. We have reason to think that the fibres which can thus be traced to this combined nucleus are afferent fibres, and that the cells composing the nucleus are the recipients of impulses reaching them along these fibres. Hence we may fitly describe the fibres as 'ending in' the nucleus; just as in a similar manner we may describe the efferent spinal accessory as 'springing from' the group of cells forming its nucleus.

All the fibres however of the roots of these three nerves do not thus end in the nucleus in question; some of them end or begin in a different way.

In sections through the bulb there may be seen just ventral to and a little lateral to the combined nucleus (Fig. 113, 4, 5, 6, IX. *a*), the circular section of a longitudinal bundle of fibres. In the hinder sections (Fig. 113, 4) the bundle is a very thin one, and still further back it is lost to view, though there are reasons for thinking that some of the fibres are continued back into the cervical cord, as far as the origin of the fourth cervical nerve or even beyond; in the more forward sections (Fig. 113, 5 and 6) it increases in diameter and may be traced forward to the front end of the combined nucleus into which it merges. It is a bundle of fibres which, starting successively in the lateral grey matter of the cervical cord and higher up in the reticular formation of the bulb, run longitudinally forwards; the bundle at first increases in size by the addition of fresh fibres at each step; but farther forwards the fibres leave the bundle to pass into the roots of the nerves of which we are speaking, especially of the glossopharyngeal, and the bundle eventually ends in front by passing into the glossopharyngeal roots. The bundle is called the *ascending root* of the glossopharyngeal, the term ascending being used since it is customary to trace such structures from below upwards, that is from behind forwards; though since the fibres in question are probably afferent fibres carrying impulses backwards from the nerves to the grey matter, 'descending' would be the more appropriate word. The bundle has also been called the ***fasciculus*** *solitarius*; and, since its position has been supposed to correspond to that of the area marked out experimentally as the respiratory centre, § 361, it has been spoken of as the *respiratory bundle*. Along its whole length this ascending root is accompanied by a quantity of grey matter, and fibres or collaterals passing off from the roots form synapses with the cells in this grey matter. Hence, though the cells do not form a compact mass such as can be called a nucleus, the grey matter in question may be regarded as the ending of the root.

As we shall see, the fibres of other afferent cranial nerve roots bifurcate, after the fashion of the fibres of a dorsal spinal root, soon after their entrance into the bulb; but this does not seem to be the case with the afferent fibres of the accessory-vago-glosso-pharyngeal roots.

But there is yet a third source of some of the fibres of the nerves of which we are speaking. In sections of the bulb above the decussation of the pyramid a patch of grey matter is seen lying in the lateral part of the reticular formation (Fig. 113, X. *m*), about midway between the ventral and dorsal surfaces. What is thus disclosed by sections is a column of grey matter, the "nucleus ambiguus" (Fig. 119, *na*), stretching about as far forwards and backwards as the combined accessory-vago-glossopharyngeal nucleus, but placed distinctly more ventrally and somewhat more laterally. (In Fig. 119, it and the combined nucleus are represented on different sides of the diagram, to avoid confusion through the overlapping of the shading.) From it fibres curve round (Fig. 113, 6, X. *m*), to join the accessory-vago-glossopharyngeal roots, but especially the vagus roots. It may therefore be considered as an additional nucleus of the vagus (and possibly of the other) roots. We have reason to think that the fibres connected with this nucleus ambiguus are efferent, and indeed motor fibres.

The roots of these three nerves then, the bulbar accessory, the vagus, and the glossopharyngeal, all leaving the surface of the brain along the line between the olive and the restiform body, and all so far alike that it is impossible upon mere inspection to say where in the series the fibres of the middle nerve, the vagus, begin and end, spring from three sources, the combined nucleus, the nucleus ambiguus, and the ascending root.

§ 618. *The Eighth or Auditory Nerve.* This nerve differs from the other nerves which we are now considering in being a nerve of special sense; its arrangements are complicated. In a view of the base of the brain (Fig. 112, C), the nerve is seen to leave the surface of the brain from the ventral surface of the fore part of the restiform body at the hind margin of the pons as two strands or roots, one of which winds round the restiform body so as to reach its dorsal surface while the other appears to sink into the substance of the bulb to the median side of the restiform body; and in a transverse section of the bulb (Fig. 114) just behind the pons the two roots may be seen embracing the restiform body, one passing on its dorsal and the other on its ventral side. The former is called the *dorsal* root (Fig. 114), or sometimes the lateral root (it has been called the posterior or inferior root); the latter is called the *ventral* root (Fig. 115), or sometimes the median root (it has

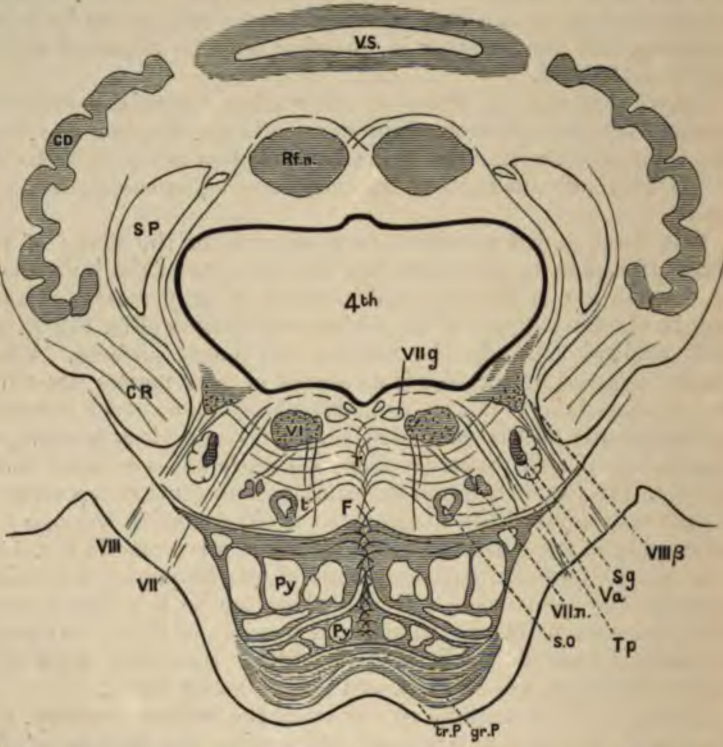


FIG. 115. THROUGH THE WIDEST PART OF THE FOURTH VENTRICLE. (Sherrington.) *Taken in the line* 115, Fig. 112.

Py. Pyramidal fibres cut transversely. *tr. P.* the superficial (ventral) transverse fibres of the pons. The shaded part of the pons (*gr. P.*) indicates grey matter mingled with the deeper transverse fibres. *F.* the fillet. *Tp.* the trapezium. *C. R.* the restiform body or inferior peduncle of the cerebellum, cut across obliquely. *S. P.* the superior peduncles of the cerebellum. *r.* raphe. *s. o.* superior olive. *C. D.* corpus dentatum of the cerebellum. *Rf. n.* the nucleus of the roof. *s. g.* tubercle of Rolando. *V. S.* section through sulcus in the vermis superior of the cerebellum. *t.* bundle from the olive to the lenticular nucleus.

VIII. the eighth or auditory nerve, its ventral or vestibular root, proceeding from VIII. *β*. the front part of the lateral auditory nucleus. VII. *n.* the nucleus of the seventh or facial nerve. VI. the nucleus of the sixth nerve. VII. *g.* fibres of the seventh nerve cut across as they sweep round the nucleus of the sixth before issuing from the pons as VII.

4th, the fourth ventricle, here roofed in by the cerebellum; the shading of the central grey matter immediately surrounding the ventricle is, for the sake of simplicity, omitted.

been called the anterior or superior root). When we come to study the ear we shall find that one division of the auditory nerve is distributed to the cochlea alone and is called the nervus cochlearis, the rest of the nerve being distributed to the utricle, saccule and semicircular canals as the nervus vestibularis. As we shall see, there are reasons for thinking that the vestibular nerve carries up to the brain from the semicircular canals impulses other than those or besides those which give rise to sensations of sound, whereas the cochlear nerve appears to be exclusively concerned in hearing; and in some structural details these two divisions of the auditory nerve differ from each other. Hence it is important to note that the cochlear nerve is the continuation of the dorsal root and the vestibular nerve the continuation of the ventral root; the former may with advantage be called the *cochlear* root, and the latter the *vestibular* root.

With these roots of the auditory nerve proper also issues, a little in front of the ventral root, the small nerve called the *portio intermedia Wrisbergi*, which goes to join the facial nerve.

The auditory nucleus, as a whole, is a broad mass, having in transverse sections of the bulb a somewhat triangular form, lying in the lateral parts of the floor of the fourth ventricle, reaching in front somewhat beyond the level of the striæ acusticæ, and overlapping behind the front parts of the nucleus ambiguus and the combined accessory-vago-glossopharyngeal nucleus; it extends laterally some distance outside the former nucleus.

The nucleus however consists of two distinct parts, a *median* or *inner nucleus* (Fig. 119, VIII. *m.*), characterized by the presence of small cells, and a *lateral* or *outer* nucleus (Fig. 119, VIII. *l.*), the cells of which are much larger, some of them being very large. The lateral nucleus is placed somewhat deeper than, ventral to, the median nucleus; it also extends farther forwards (Figs. 114 and 115, VIII. β), so that the front end of the whole nucleus is furnished by the lateral nucleus alone, which at its front end occupies a more dorsal position than at its hind end.

Moreover this auditory nucleus thus placed in the floor of the fourth ventricle is the nucleus not of the whole auditory nerve, but of the vestibular nerve only. At the convergence of the cochlear and vestibular roots on the ventral surface of the restiform body is placed a group of cells, forming a swelling which in its general appearance and in some of the characters of its cells is not unlike a ganglion on the dorsal root of a spinal nerve. This is called the *accessory nucleus*. The cochlear root further bears a dorsal swelling, due to the presence of cells, *the tuberculum acusticum*, which, small in man, is in some animals conspicuous.

When we trace centralwards into the brain the fibres of the cochlear root (Fig. 114) we find that these, like the fibres of a spinal dorsal root upon their entrance into the spinal cord, bifurcate into ascending and descending branches. The branches which are short end, the ascending in connection with the cells of the accessory nucleus, the descending in connection with the cells of the tuberculum acusticum and also with those of the accessory nucleus. These two bodies in fact, the accessory nucleus and the tuberculum acusticum, form together the ending or nucleus of the cochlear root, and might be called the 'cochlear nucleus.' Hence the fibres which winding round the lateral and dorsal surface of the restiform body appear to be a continuation of the cochlear root are not really so; they are fibres starting from the cells of the tuberculum acusticum and accessory nucleus, which cells serve as a relay. Reaching the dorsal surface of the restiform body, these fibres form on the floor of the fourth ventricle the *striæ acusticæ* (Fig. 112, *str.*), and, though their course has not as yet been completely made out, appear to end in certain regions of the tegmentum, some being said to run into the fillet. Many at least of these fibres cross over to the opposite side. From the accessory nucleus also start a number of fibres which running transversely in the ventral region of the tegmentum, dorsal to the transverse fibres of the pons, form what is called the trapezium (Fig. 115, *Tp.*). Most of these fibres cross over to the opposite side and end or are connected by collaterals with various collections of grey matter in the tegmental region. Thus, as we shall see, the cochlear nerve, by means of relays first in the cochlear nucleus and then in the grey matter of the tegmental region, becomes connected with the cerebral hemispheres.

When we trace the vestibular root (Fig. 115) inwards we find that making no connections at all with the cochlear nucleus, it passes (Fig. 115, VIII) to the median side of the restiform body, between it and the ascending root of the fifth nerve, and so reaches the vestibular nucleus. Its fibres, like those of the cochlear nerve, all bifurcate, the branches taking an ascending and a descending course. The descending branches appear to end almost entirely in connection with the cells of the median nucleus. Some of the ascending fibres also end in the same median nucleus, but the majority of these end in connection with the cells of the lateral nucleus. From this lateral nucleus, which lies on the median side of the restiform body, fibres pass up to the cerebellum, constituting what is sometimes spoken of as "the median division of the restiform body"; and the nucleus may perhaps be considered as a relay for the vestibular fibres on their way to the cerebellum, analogous to the relay of the vesicular cylinder between the dorsal roots of spinal nerves and the direct cerebellar tract. It is probable however that some of the ascending fibres of the vestibular nerve do not end, after a short course, in the lateral nucleus, but passing by the cells of the nucleus pursue a longer unbroken course along the median division of the restiform body up to the cerebellum, where they end in the grey matter known as the "nucleus of the roof," and apparently in that of the opposite side. These ascending fibres thus constitute a connection, direct or indirect, between the auditory (vestibular) nerve and the cerebellum, the physiological significance of which we shall see later on.

From the cells both of the lateral and median nucleus fibres pass to the tegmental region of the opposite side, some taking part in what we shall speak of hereafter as the posterior longitudinal bundle. Thus by the relay of the vestibular nucleus (median and lateral) the vestibular nerve is brought into connection with the tegmental region.

Lastly, we may add that the fibres of the peculiar *portio intermedia Wrisbergi* appear according to recent researches to be

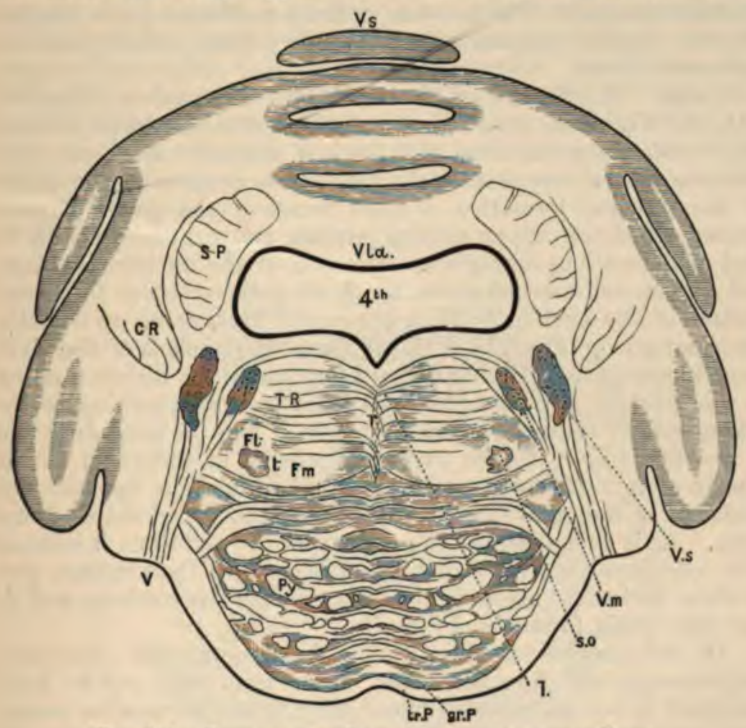


FIG. 116. THROUGH THE PONS AT THE EXIT OF THE FIFTH NERVE. (Sherrington.)

(*Taken in the line* 116, Fig. 112.)

C. R. Remains of restiform body. *S. P.* superior peduncle of the cerebellum. *F. m.* median, *F. l.* lateral fillet. *T. R.* tegmental reticular formation. *tr. P.* superficial transverse fibres of the pons. *l.* posterior longitudinal bundles. *V. s.* superior vermis; sections of three folia are shewn, one being detached; between them the intervening sulci laid open by the section are seen. *Vl. a.* valve of Vieussens or anterior velum. *r.* raphe. *Py.* Pyramidal fibres. *gr. P.* grey matter of the pons. *s. o.* superior olive. *t.* placed on the left side indicates the position of a bundle of longitudinal fibres which may be traced forward into the subthalamic regions. *V. m.* motor nucleus. *V. s.* sensory nucleus, and *V.* roots of the fifth nerve.

4th, fourth ventricle; shading of central grey matter omitted as in Fig. 115.

connected with the geniculate ganglion lying on the facial nerve, in the Fallopian canal, in the same way that the afferent fibres of a spinal nerve are connected with the ganglion on the dorsal root. The cells of the geniculate ganglion give rise by T-pieces to central and peripheral fibres. The peripheral fibres run along the facial nerve to form part of the chorda tympani; the central fibres form the portio intermedia (which may therefore be compared to the dorsal root of a spinal nerve) and entering the bulb bifurcate like dorsal root-fibres, both ascending and descending branches ending in the grey matter surrounding the ascending root of the glossopharyngeal. The nerve is in fact an afferent nerve supplying the chorda tympani with its sensory (but probably not its gustatory) fibres.

§ **619**. *The Seventh or Facial Nerve.* The nucleus (Fig. 119, VII. and Figs. 114, 115, VII. *n.*), of this nerve, narrower in front than behind, reaches from the level of the striæ acusticæ some distance into the region of the pons, and occupies in the midst of the reticular formation, a little dorsal of the patch of grey matter called the upper olive, a position corresponding closely to that of the nucleus ambiguus. The cells of the nucleus are large, and possess well-marked axons, which are gathered up at the dorsal surface of the nucleus to form the root. This, rising up dorsally, describes a loop (Fig. 115, VII. *g.*) round the nucleus of the sixth or abducens nerve, running forward for some little distance dorsal to that nucleus, and then descends again ventrally, passing to the lateral side of its own nucleus, between it and the ascending root of the fifth (*Va*); it thus gains the surface of the brain at the hinder margin of the pons, lateral to the abducens, opposite the front end of the groove between the olivary body and the restiform body. As it thus encircles the nucleus of the abducens, it looks as if it were receiving fibres from that body; but the evidence goes to shew that these fibres simply pass through the nucleus, and do not take origin from any of its cells.

Of the muscles supplied by the facial nerve, the orbicularis palpebrarum and frontalis stand apart from the other facial muscles; in certain cases of facial palsy these two muscles escape. And indeed the fibres supplying them are derived not from the facial nucleus, but from the hind part of the nucleus of the third nerve. In consequence, this part of the third nucleus is often called the upper nucleus of the facial nerve.

§ **620**. *The Sixth or Abducens Nerve.* This nerve starts from a compact oval nucleus (Fig. 119, VI.), lying at the level of the hinder part of the pons, and therefore of the front part of the fourth ventricle, in the central grey matter of the floor of the ventricle, or rather just between it and the reticular formation, a little on one side of the median line (Fig. 115, VI.). A slight swelling of the floor of the fourth ventricle, eminentia teres, marks its position (Fig. 119, *e. t.*). The nucleus contains fairly large nerve-cells, with distinct axis-cylinder processes. These are gathered at the median side of the nucleus to form the thin root, which passing ventrally and laterally, at some little distance from the median raphe, through the reticular formation, runs backward above the pyramidal bundles of the pons, and finally comes to the surface at the hinder edge of the pons, opposite the front end of the pyramid (Fig. 112, C).

§ **621**. *The Fifth or Trigeminal Nerve.* This nerve, as it comes to the surface on the ventral aspect of the pons (Fig. 112, C), near the front edge, at some distance from the median line, consists of two parts, a smaller motor root and a larger sensory root, the latter bearing the large ganglion of Gasser; and the origin of the nerve is in many ways complex. Both roots may be traced in an oblique direction (Fig. 116, V.) inwards and backwards through the pons towards the dorsal and lateral surface of the reticular formation beneath the floor of the front part of the fourth ventricle, the smaller motor root taking up a position median to the larger sensory root.

Here the motor root takes origin in part from a collection of

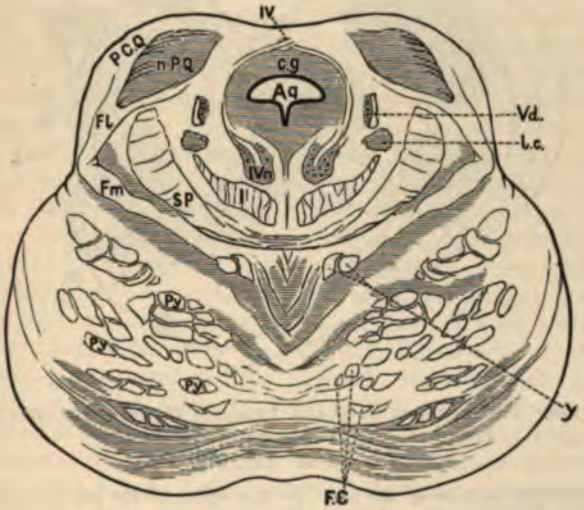


FIG. 117. THROUGH THE FORE PART OF THE PONS. (Sherrington.)
(*Taken in the line* 117, Fig. 112.)

Py. Pyramidal fibres. *F. C.* Fibres from the frontal cortex. *S. P.* superior peduncle of the cerebellum. *F. m.* median portion, *F. l.* lateral portion of the fillet. *l.* posterior longitudinal bundles. *P. C. Q.* Posterior corpora quadrigemina. *y.* Fibres which become detached from the fillet, and further forward form (the innermost) part of the pes of the crus. *l. c.* locus cæruleus. *n. P. Q.* nucleus of the posterior corpora quadrigemina; the outline is made too sharp. IV. bundles of the fourth nerve decussating, IV. *n.* its nucleus. V. *d.* descending root of the fifth nerve. *Aq.* the aqueduct. *c. g.* the region of central grey matter.

nerve-cells (Figs. 119 and 116, V. *m.*), which may be regarded as its nucleus; but in part only, for this is not the whole origin of the motor root.

From the level of the nucleus there stretches forwards as far as the level of the anterior corpora quadrigemina a bundle of longitudinal fibres which, since it is usually traced from the front backwards until it passes into the root of the nerve, is spoken of as *the descending root* of the fifth nerve. This descending root begins as a few scattered bundles of fibres at the level of the anterior corpora quadrigemina, in the peripheral lateral part of the central grey matter surrounding the aqueduct, dorsal and lateral (Fig. 118, V. *d.*), to the nucleus of the third nerve (Fig. 118, III. *n.*). From thence the fibres pass backward, augmenting in number, and soon form a compact bundle, semilunar in transverse section, lying lateral to the fourth nerve as this is rising dorsally (Fig. 117, V. *d.*); still increasing in number in their course backward they gradually assume a more ventral position as the aqueduct opens into the

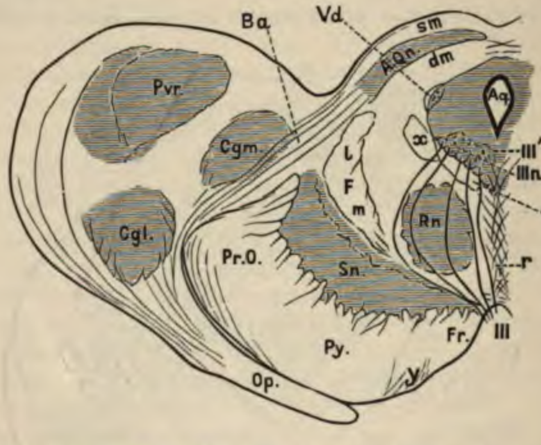


Fig. 118. Through the Crus and Anterior Corpora Quadrigemina. (One half only is shewn.) (Sherrington.)
(*Taken in the line* 118, Fig. 112.)

Py. the pyramidal portion of the pes. *Fr.* the region of the pes occupied by fibres from the frontal portion of the cortex. *Pr. O.* the region occupied by fibres coming from the occipital portion of the cortex. *y.* fibres coming from the fillet. *Op.* the optic tract. *F.* the fillet, *l.* the lateral portion, *m.* the median portion. *l.* the posterior longitudinal bundle. *B. a.* the brachium of the anterior corpus quadrigeminum. *x.* fibres from the posterior commissure of the cerebrum. *r.* raphe. *S. n.* substantia nigra. *R. n.* red nucleus. *C. g. l.* lateral, and *C. g. m.* median corpus geniculatum. *Pvr.* pulvinar of optic thalamus. *A. Q. n.* nucleus or grey matter of anterior corpus quadrigeminum. III. *n.* nucleus of III. third nerve. III′. Rootlets from the dorsal part of III. *n.* the nucleus of the third nerve which cross the median line to emerge with rootlets derived from the nucleus of the opposite side. *s. m.* superficial layer of fibres of the ant. corp. quad. *d. m.* deep layer. V. *d.* descending root of the fifth nerve. *Aq.* aqueduct surrounded by cerebral grey matter.

fourth ventricle. All along its course this descending root has attached to it large (70 μ or more in diameter), sparse, spheroidal nerve-cells, of striking appearance, from which its fibres take origin. This elongated group of cells is sometimes called the 'upper' motor nucleus, the more compact mass from which the rest of the motor root arises being called the 'lower' motor nucleus.

When the fibres of the afferent sensory root are traced backward from the Gasserian ganglion, each fibre is found like other afferent root fibres, to bifurcate into an ascending and descending branch. The ascending branches are short and end in a nucleus, the sensory nucleus (Figs. 119 and 116, V. *s.*) which lies lateral to the (lower) motor nucleus.

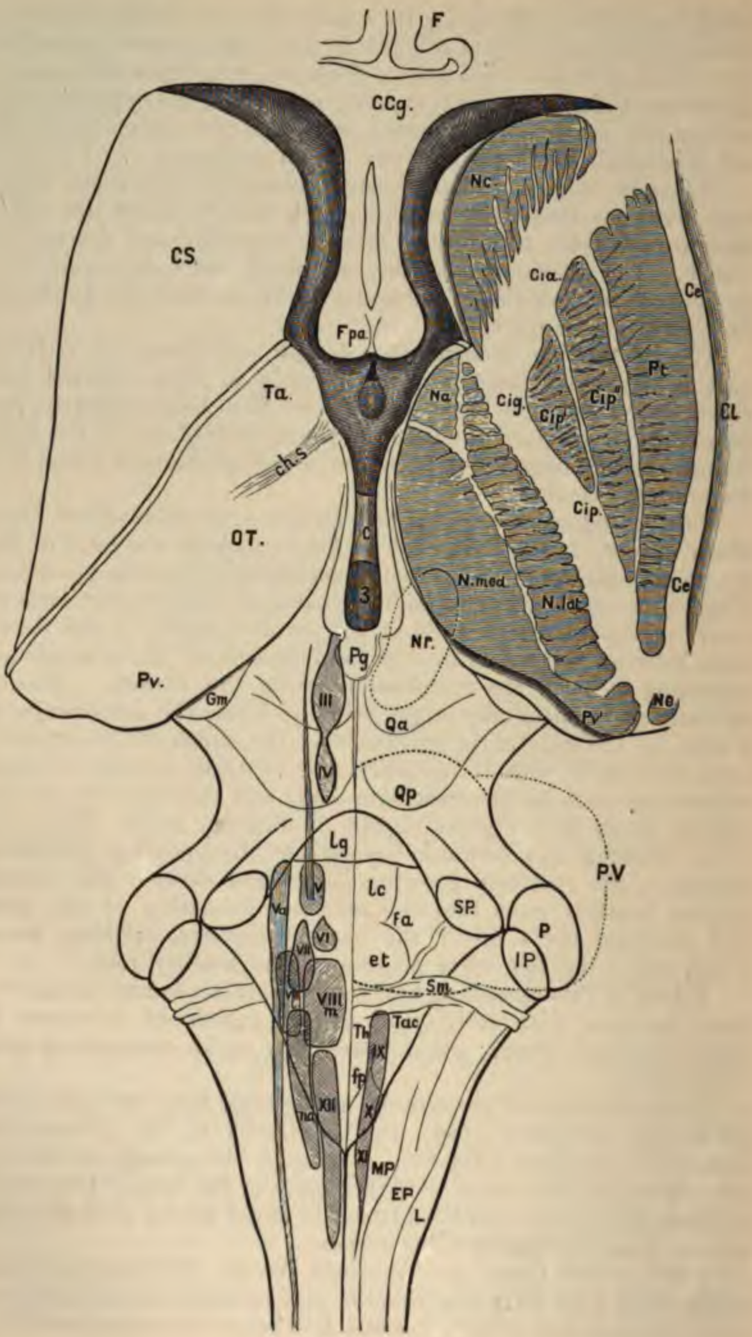
The descending branches are longer and form the striking tract of fibres to which we have already so often referred, and which, owing to its being usually traced from below upwards, has unfortunately received the name of the *ascending* root of the fifth, though the impulses which its fibres normally transmit travel in a descending direction.

This ascending root begins as a bundle or bundles of few fibres which may be traced backward as far as at least the level of the second cervical nerve, and is soon conspicuous in transverse sections (Fig. 113 *et seq.*, V. *a.*) as a semilunar patch of white matter forming a sort of cap on the outside of the swollen caput of the dorsal horn, between this structure and the longitudinal fibres which are beginning to form the restiform body on the surface. Passing upwards, and continually augmenting in bulk, the root clings, as it were, to the gelatinous substance of the caput of the posterior horn, and sinks with it inwardly and ventrally as this becomes covered up first by the restiform body and subsequently by the issuing trunk of the great eighth or auditory nerve (Figs. 114, 115). Passing still forward, beyond the disappearing gelatinous substance, the root still growing larger and divided into several distinct bundles, runs into the reticular formation of the pons and, reaching the level of the sensory nucleus, suddenly bends round and joins the other portion of the sensory root.

Fibres of this ascending root send collaterals to and themselves form synapses with cells lying in the gelatinous substance to which the root clings; other fibres may make connections with other cells.

From the cells of the sensory nucleus and from the cells of the gelatinous substance axons may be traced to the fillet of the opposite side; these cells form a relay in the passage of afferent impulses along the nerve to higher parts of the brain. Collaterals of these fibres have also been traced to motor nuclei, thus affording a simple mechanism for reflex action.

§ **622**. *The Fourth or Trochlear Nerve.* The nucleus of this nerve (Fig. 119, IV.) is a column of somewhat large multipolar cells on each side of the median line below the aqueduct (Fig.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CCg.
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Fig. 119.

FIG. 119. DIAGRAM TO ILLUSTRATE THE POSITION OF THE NUCLEI OF THE CRANIAL NERVES. (Sherrington.)

The brain is supposed to be viewed from the dorsal aspect, the cerebral hemispheres and cerebellum having been cut away. The nuclei are represented as if seen through transparent material. On the right side, the corpus striatum and optic thalamus have been cut away horizontally to some little depth in order to shew their internal structure.

L. lateral, *E. P.* external posterior and *M. P.* median posterior column of the cord. *I. P.* inferior peduncle, *S. P.* superior peduncle, and *P.* middle peduncle of the cerebellum, all cut across. The dotted curved lines, upper and lower, on the right half of the figure to which the dotted line *P. V.* outside the figure points, mark the upper and lower boundaries of the pons on the ventral aspect.

The outline of the fourth ventricle is shewn by a bold thick line. In the floor of the ventricle are shewn, on the right half:—*fp.* fovea posterior. *Th.* trigonum hypoglossi. *T. ac.* trigonum acusticum. *e. t.* eminentia teres. *s. m.* striæ medullares or acusticæ. *f. a.* fovea anterior. *l. c.* locus cæruleus. *l. g.* valve of Vieussens.

Qp. posterior and *Qa.* anterior corpus quadrigeminum. *Pg.* pineal gland. *Nr.* the outline of the red nucleus. 3, the third ventricle, in which *C* indicates the middle or soft commissure. *F. p. a.* the pillars of the fornix, behind which is indicated in the cavity of the third ventricle the hollow of the infundibulum. *C. C. g.* the genu of the corpus callosum, between which and the fornix the cavity often called the fifth ventricle is indicated. *F.* portion of convolution of frontal hemisphere cut across.

On the left side are shewn:—*C. S.* corpus striatum. *O. T.* optic thalamus. *Pv.* pulvinar. *T. a.* Tuberculum anterius. *ch. s.* choroidal sulcus marking the place of reflection of the choroidal plexus. On the right side are exposed:—*NC.* head of, *Nc,* end of tail of nucleus caudatus. *Cip', Cip''* the two parts of the globus pallidus, and *Pt,* putamen of the nucleus lenticularis. *N. a.* anterior nucleus. *N. med.* median nucleus, *N. lat.* lateral nucleus and *Pv'.* pulvinar of the optic thalamus. *Cia.* front limb, *Cig.* knee or genu, *Cip.* hind limb of internal capsule. *Ce.* external capsule. *Cl.* claustrum.

The numerals III. to XII. indicate the nuclei of the respective cranial nerves, all shewn on the left side with the exception of the accessory-vago-glossopharyngeal IX. X. XI., which to avoid confusion is placed on the right side. *V.* is the motor nucleus of the fifth nerve with the descending root, *V. a.* the sensory nucleus of the same with the long ascending root. VIII. *m.* median nucleus, VIII. *l.* lateral nucleus of the auditory nerve. *n. a.* nucleus ambiguus. The ascending root of the ninth nerve is seen at the hind end of the combined nucleus of IX. X. XI.

117, IV. *n.*), reaching from the level of the junction of the anterior and posterior corpora quadrigemina to the hinder level of the latter body.

The root, starting from the lateral surface of the nucleus, does not take at first a ventral direction, but sweeps laterally and dorsally in the outer layers of the central grey matter (Fig. 117), and so curving round to the dorsal surface reaches the valve of Vieussens, where in the median line it decussates with its fellow in the substance of the valve. In thus decussating it affords a contrast with the other cranial nerves. The afferent cranial nerves do not decussate at all; in the case of the efferent cranial nerves, the third of which we are about to speak, the motor root of the fifth, the seventh, the motor root of the vagus and glossopharyngeal and the hypoglossal, some of the fibres starting in the nucleus of one side are described as crossing over to join the nerve of the other side; but such a decussation is very partial and is not admitted by all observers in all the above cases. The decussation of the fourth nerve however is complete and obvious, and takes place at some distance from the nucleus of origin. Leaving the surface of the brain in the valve, the nerve takes a superficial course curving (Fig. 112, B) laterally and ventrally, and makes its appearance in a ventral view of the brain at the front edge of the pons, on the lateral edge of the crus (Fig. 112, C).

§ **623**. *The Third or Oculomotor Nerve.* The nucleus of this nerve (Fig. 119, III., 118, III. *n.*) is a column of, for the most part, fairly large multipolar cells lying on each side close to the median line, in the grey matter of the central canal, just dorsal to a bundle of fibres which we shall speak of as the longitudinal posterior bundle; it reaches from the level of the posterior commissure in the third ventricle to the level of the junction of the anterior and posterior corpora quadrigemina. In a section taken through its middle (Fig. 118) the nucleus is seen to give off fibres which run vertically towards the ventral surface, traversing the tegmentum and a body (*Rn.*) which we shall presently speak of as the "red nucleus," but apparently making no connections with these structures, and pierce the median edge of the pes, emerging (Fig. 112, C) on the surface to the median side of each crus. As we shall see later on, this nerve is now exclusively efferent, whatever it may have been in more primitive beings. The nucleus as a whole may be divided into groups of cells, or smaller nuclei, of which a single median group and a lateral group on each side alone give origin to the fibres of the nerve. Two other groups characterized by being made up of small cells do not give origin to any of the fibres of the nerve, and therefore do not properly belong to the nucleus. We have further seen (§ 619) that the hind part of the nucleus gives rise to some of the fibres of the facial nerve.

As has already been stated some few of the fibres arising from the nucleus of one side cross over to join the nerve of the other side. A considerable number of decussating fibres may be seen in the immediate neighbourhood of the nucleus at its ventral aspect in the median line; but the fibres thus decussating are not the fibres of the nerve arising in the nucleus.

This nerve has special relations with the optic tract, but of these we shall speak when we come to deal with the functions of the nerves.

§ **624**. In attempting to understand the nature and relations of these cranial nerves, it must be borne in mind that, while morphological studies lead us to believe that, as the vertebrate body has been developed out of an invertebrate ancestry, so the brain of the vertebrate has arisen by a series of modifications from the nervous structures placed at the head and around the mouth of an invertebrate, the same studies teach us that such an evolution has been accomplished by means of profound changes. We have, for instance, reason to think that the mouth of the vertebrate does not correspond to the mouth of the invertebrate, but is a new structure, whose appearance has been accompanied by a considerable dislocation of parts. We must accordingly expect to find the indications of a segmental arrangement greatly obscured on the one hand by transposition, and on the other by fusion.

The twelfth or hypoglossal nerve is one whose nature seems fairly simple. It is in function exclusively an efferent nerve. The large cells, with conspicuous axons, which characterize its nucleus, are exactly like those of the ventral horn of the spinal cord which give origin to the fibres of a ventral root. The nucleus moreover in its position corresponds to part of the ventral horn of the spinal cord, if we take into account the shifting involved in the decussation of the pyramids, and in the new developments of the bulb. If we compare Fig. 113 with any section of the cord, we see that the hypoglossal nerve corresponds to a ventral root of the spinal cord, but that the fibres, after leaving the cells from which they take origin, traverse in the former a large tract, and in the latter case a small tract of tissue. Whether the whole nerve corresponds to the fibres of several segments fused together, or to those of one segment spread out longitudinally, is for our present purposes of secondary importance.

Recognizing the hypoglossal nerve as the homologue of a spinal ventral root, we may go on to claim the nuclei of the third and fourth nerves as similar groups of cells of the ventral horn, giving rise to ventral roots. The position of the nuclei, the character of the cells, the function of the fibres, all support this view. The case is perhaps not so clear as that of the hypoglossal nerve, since there are reasons for thinking that these nerves have undergone in the course of evolution greater changes than has the hypoglossal nerve; still these reasons do not oppose the above conclusion.

The nucleus of the exclusively motor sixth nerve does not exactly correspond to those of the third and fourth in position; but we may probably place it in the same series with them. Thus we have in succession, the third, fourth, sixth, and twelfth nerves, with their respective nuclei, as the ventral roots of nerves of their several segments.

In the fifth nerve, the dislocation and fusion spoken of above has introduced difficulties. The motor nucleus, with the fibres of the motor root to which it gives origin, has by some been considered as homologous to the series just described; but it is at once obvious that we cannot look upon this great fifth nerve as corresponding to one spinal nerve, with its ventral and dorsal root, great as the superficial resemblance seems to be. The features of the remarkable so called "ascending" but in reality descending root forbid this. The fibres of this root may be traced back, as we have said, to the very beginning of the bulb, and indeed into the spinal cord beyond; they are not connected with any distinct collection of nerve-cells, such as could be called a nucleus; but the bundle of fibres clings, as we have seen, to the gelatinous substance of the dorsal horn of the spinal cord and to the continuation of this along the bulb, and the fibres end in connection with the cells of this substance. The root, therefore, corresponds to part at least of the dorsal root of a spinal nerve; and we have now experimental proof, that the trophic centres of these fibres are to be found in the cells of the Gasserian ganglion.

But if this "ascending" root be of the nature of a dorsal root, we can hardly suppose that it belongs to a single segment, or is the complement of the motor root alone; in it, most probably, the dorsal fibres of several segments are blended together. Further, we may perhaps infer that the other fibres of the sensory root which end directly in what we have called the sensory nucleus, are in nature distinct from the fibres of the ascending root; and if so, difficulties arise as to the nature and homologies of the nucleus in question. These, however, we must not discuss here, nor can we enter into the question of how the descending root though motor differs from the rest of the motor root. We have said enough to shew that this fifth nerve is extremely complex, and that its apparent conformity to a simple spinal nerve is in reality misleading.

The fibres of the vagus, glossopharyngeal, and bulbar accessory, taken together, are partly efferent, partly afferent. The combined nucleus of these three nerves, the cells of which are small and devoid of conspicuous axis-cylinder processes, is usually regarded as a sensory nucleus, and in the diagram, Fig. 119, is shaded accordingly. It may perhaps be compared to the sensory nucleus of the fifth. Thus, the ascending root, or fasciculus solitarius, presents many analogies with the ascending root of the fifth, and we are led to regard this as, like it, a gathering of certain afferent fibres of the dorsal roots of several segments; in its case also the term ascending is misleading; both are descending branches of the bifurcating afferent root-fibres. But there are many difficulties in connection with this nucleus, as with the fifth. We must not enter into a detailed discussion concerning them, but may remark that we have here perhaps to deal with complexities due to the fact that certainly many vagus and glossopharyngeal fibres, and probably some of those of the fifth, are splanchnic in function.

The nucleus ambiguus contains large conspicuous cells and we must regard it as a motor nucleus, especially of the vagus fibres. We may also perhaps place it and the nucleus of the seventh nerve in the same category, and further class with them the motor nucleus of the fifth, looking upon all three as so many detached portions of grey matter, corresponding to some part of the ventral horn of the spinal cord. Whether they are exactly homologous to the hypoglossal nucleus, and their fibres to simple ventral roots, is not so clear.

Lastly, the auditory nerve, both from its character as a nerve of special sense and from the remarkable features of its nuclei, is even more difficult. Most probably it results from the fusion of more roots than one; but it is impossible at present to obtain a clear conception of the nature of the whole nerve.

2. *The Superficial Grey Matter.*

§ 625. The whole of the surface of each cerebral hemisphere for some little depth inwards consists of grey matter, possessing special characters; this is called the cortical grey matter, or the *cortex cerebri*, or shortly and simply the *cortex*. As we shall see, by its histological and still more by its physiological features, it stands apart from all other kinds of grey matter.

The whole of the surface of the cerebellum is also covered with grey matter, which, while possessing features of its own, so far resembles the cerebral cortex in its histological characters that it too has been spoken of as cortex, as the cortex cerebelli. By its functional manifestations, however, it differs widely from the cerebral cortex; and since there are many advantages in being able to use the word cortex in connection with the cerebrum only, it is desirable not to speak of a cerebellar cortex, but to employ the term "superficial grey matter of the cerebellum."

The third ventricle and the hinder part of the fourth ventricle are not roofed in by nervous material, and possess no superficial grey matter at all. In the corpora quadrigemina, which form the roof of the aqueduct or cavity of the mid-brain, grey matter is present and possesses, in the case of the anterior corpora quadrigemina at least, characters to a certain extent analogous to those of the cortex and to the cerebellar superficial grey matter; but it will be best to consider the grey matter of these bodies as belonging to another category.

3. *The Intermediate Grey Matter of the Crural System.*

§ 626. We have seen (§ 603) that the crura cerebri form the prominent part of a system of longitudinal fibres stretching from each cerebral hemisphere to the bulb and to the spinal cord. This system of fibres, upon which we may consider the various parts of the brain to be as it were founded, we may speak of as the crural system. It is, it is true, not one continuous strand, but a number of different strands, having different beginnings and endings; but these all contribute to the crura and are so far alike as to justify us in considering them as a system. The cortical grey matter of each hemisphere is, as we shall see, connected with various parts of this system, and in one sense we may regard this system as beginning in the cortex of each hemisphere, and ending in the spinal cord. But certain masses of grey matter in the hemisphere not strictly cortical, and several important masses and areas of grey matter lying between the hemisphere and the cord, are connected with the system; and these we may speak of as the "intermediate grey matter of the crural system."

Corpus striatum and *optic thalamus.* Of all these several collections of grey matter, the largest, most conspicuous, and perhaps the most important are the two masses in the front part of the system known as the corpus striatum and optic thalamus. The former is, as we have seen (§ 602), a development of the wall of the cerebral vesicle, the latter a development of the wall of the vesicle of the third ventricle. They are therefore of different origin; although in the course of the growth of the brain they become closely attached to each other, they are at the outset quite separate and distinct. Moreover, as we shall see, they differ from each other so essentially, in their nature and relations, that they cannot be considered as homologous bodies; and the term "basal ganglia" often applied to them is therefore unfortunate. Nevertheless it will render the description of their topographical relations easier, if for a little while we consider them together.

When the lateral ventricle is laid open from above, part of the corpus striatum is seen projecting into the cavity of the ventricle. In front the projecting part is broad, forming the lateral wall and part of the floor of the ventricle, and to its median side lies the cavity of the ventricle, separated from its fellow by the septum lucidum. Farther back the projecting part, becoming gradually narrower, assumes a more lateral position and passes into the descending horn. In this part of its course there lies on its median side, separated from it by a narrow band called the tænia semicircularis or stria terminalis, the optic thalamus, a narrow strip of the surface of which is seen projecting outside the edge of the choroid plexus. If now, not only both lateral ventricles be laid open by removal of the corpus callosum and the fornix with the velum interpositum and choroid plexus be taken away, so as fully to expose the third ventricle, but also, in order to obtain a better view, the whole of the hinder part of the cerebrum containing the posterior horns of the lateral ventricle be completely cut away, it is seen (Fig. 119) that the two optic thalami (*O. T.*) present themselves as two large oval bodies, placed obliquely athwart the diverging crura cerebri and converging in front to form the immediate walls of the third ventricle. In front and to the sides of the optic thalami are seen the corpora striata (*C. S.*) forming anteriorly the lateral walls of the two lateral ventricles, and diverging behind to allow of the interposition of the optic thalami. On each side of the brain then these two bodies, the corpus striatum and optic thalamus, appear as two masses of grey matter placed on the crus cerebri as this, diverging from its fellow, begins to spread out into the cerebral hemisphere, the corpus striatum being placed somewhat in front of the optic thalamus. The relations of the two bodies moreover are such that while the optic thalamus alone forms the wall of the third ventricle to which it properly belongs, and the corpus striatum forms part of the wall of the lateral ventricle to which it in turn properly belongs, the optic thalamus also projects into and seems to form part of the wall of the lateral ventricle, though at its origin it had nothing to do with the cerebral vesicle.

We spoke just now of these bodies as being placed on the crura cerebri, but though their dorsal surfaces thus project from the dorsal surface of the diverging crura, a large portion of each body is, so to speak, imbedded in the substance of the diverging crus, and what is seen in the above surface view is only a part of each body, and indeed, in the case of the corpus striatum, only a small part. In order to understand the nature and relations of these two important bodies we must study sections taken through a cerebral hemisphere in various planes (Figs. 120—127).

Each crus is made up, as we have seen, of a dorsal portion or tegmentum consisting largely of grey matter, and a ventral portion or pes consisting exclusively of longitudinally disposed fibres. The tegmentum ends partly in structures lying ventral to the thalamus, partly in the thalamus itself; and we may for the present leave this part of the crus out of consideration. The fibres of the pes, while continuing their oblique course forwards and outwards, soon rise dorsally by the side of the thalamus, and hence, in a transverse dorso-ventral section at the level of the hind part of the thalamus (Fig. 120), are seen leaving their previous position ventral to the substantia nigra (*Sn.*) and passing (*Cip.*) by the side of the thalamus on their way to the central white matter of the hemisphere. In this part of their course they form a thick strand separating the thalamus (*ln.*) from a large mass of grey matter which, roughly triangular in section, is divided by partitions of white matter into three parts (*Gp′*, *Gp″*, *Pt.*), and of which we shall speak directly as the nucleus lenticularis.

If instead of taking a transverse we take a longitudinal dorso-ventral (or as it is called sagittal) section (Fig. 126) we find that the fibres forming the strand in question do not continue parallel to each other as they rise dorsally but diverge in a radiating manner, forming the so-called corona radiata. If again we take horizontal sections at proper levels (Figs. 119, 125), we find that this strand or rather thick band of dorsally directed radiating fibres not only stretches (*Cip.*) between the thalamus and the grey mass just spoken of, but reaching farther forward passes (*Cia.*) between the same grey mass on the lateral side and another grey mass (*Nc.*) on the median side, the latter from its position being

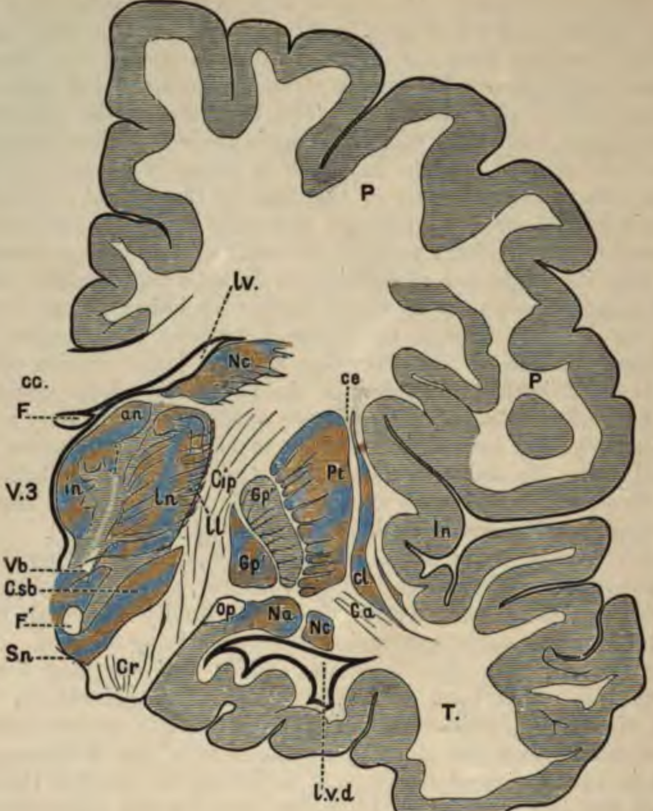

Fig. 120. Diagrammatic Outline of a Transverse Dorsoventral Section through the Right Hemisphere (Man) at level posterior to the knee of the internal capsule. (Natural size.) (Sherrington.)

Nc. nucleus caudatus; in the upper part of the figure the section of the nucleus is through the narrower portion which succeeds the wider front end or head; in the lower part of the figure the section passes through the tail of the nucleus near its end, and this portion of it has for the sake of clearness been sundered from the grey matter of *Na*, nucleus amygdalæ, more distinctly than in reality is the case. *Gp'*, *Gp''* globus pallidus, seen here in two segments, and *Pt.* putamen of nucleus lenticularis. *an.* the anterior, *in.* the inner, and *ln.* the lateral nucleus of the optic thalamus; at *ll.* is seen the "latticed layer" lying next to *Cip.*, the posterior limb of the internal capsule, and containing many strands of fibres which mingle with it. In the thalamus between the anterior and internal nuclei on the one hand and the lateral nucleus on the other is a layer shaded less deeply in the figure, representing the internal medullary lamina of the thalamus, consisting largely of white matter. Other collections of white matter within the thalamus are *Vb*, the bundle of Vicq. d'Azyr and *F'* the lower end of the anterior pillar of the fornix. *F.* The upper end of the anterior pillar of the fornix, below *cc* the corpus callosum. *Csb.* corpus subthalamicum, forming a fairly continuous mass with the thalamus; *Sn.* substantia nigra. *cl.* claustrum; *ce.* external capsule. *Ca.* terminal portion of anterior commissure. *In.* the insula or island of Reil. *lv.* the lateral ventricle; *l. v. d.*

descending horn of lateral ventricle; *V.* 3. in the position of the third ventricle; the outlines of the cavities are made diagrammatically distinct by thick black lines. *Op.* optic tract; *P. P.* Parietal lobe. *T.* Temporal lobe.

evidently the part of the corpus striatum which projects into the lateral ventricle. The same horizontal sections further teach us that the front part of the band (*Cia.*) is bent at an angle upon the hind part (*Cip.*).

It appears then from these sections that the fibres of the pes as they rise up dorsally into the hemisphere spread out in the form of a fan bent upon itself. This fan-like expansion of the pes is called the *internal capsule*, the angle formed by the bend being called its *genu* or *knee*, (*Cig.*) the part in front of the knee the *front limb*, and the part behind the knee the *hind limb*. And horizontal sections at levels more dorsal than those given in Figs. 119—125 would shew that the fibres composing this fan-like internal capsule, as they rose dorsally, curved away in various directions to reach nearly all parts of the surface of the hemisphere. We may add that though the internal capsule is mainly composed of fibres which thus stretch all the way from the cerebral cortex to the pes of the crus, it also contains other fibres of which we shall speak later on.

§ **627**. The grey mass separated from the thalamus by the hind limb of the internal capsule is called as a whole the *nucleus lenticularis*, since in horizontal section it presents a certain though distant resemblance to a lens. Of the three divisions into which it is split up by the partitions of white matter, the two median ones *Gp′*, *Gp″*. are spoken of together as the *globus pallidus*, the name being given to them on account of their paler colour. The third, lateral division *Pt.*, is called the *putamen*. The use of these two names for the two different parts of the one body appears to be justified by the different connections and features of the two parts.

The grey mass which in a horizontal section (Fig. 119, *Nc.*) is separated from the nucleus lenticularis by the front limb of the internal capsule, and which projects into the lateral ventricle, is called the *nucleus caudatus*. The nucleus caudatus and the nucleus lenticularis form together the corpus striatum; the former, since it projects into the lateral ventricle, being the part of the corpus striatum seen when the lateral ventricle is laid open, is sometimes spoken of as the intraventricular portion of the whole body, while the nucleus lenticularis, which is wholly hidden in the hemisphere and in no part projects into the lateral ventricle, is called the extraventricular portion.

But only a part, indeed only a relatively small part, of the nucleus caudatus is disclosed in such a horizontal section; to learn the somewhat peculiar form and relations of the whole nucleus a number of sections of a hemisphere taken in different planes must be studied; and these will at the same time explain why the nucleus is called 'caudatus.' These teach us that the nucleus has somewhat the form of a comma (Fig. 123). The thick rounded head forms the lateral wall of the front part of the lateral ventricle; thence the body passes backward, narrowing rapidly and diverging somewhat laterally; in its course it arches over the nucleus lenticularis,

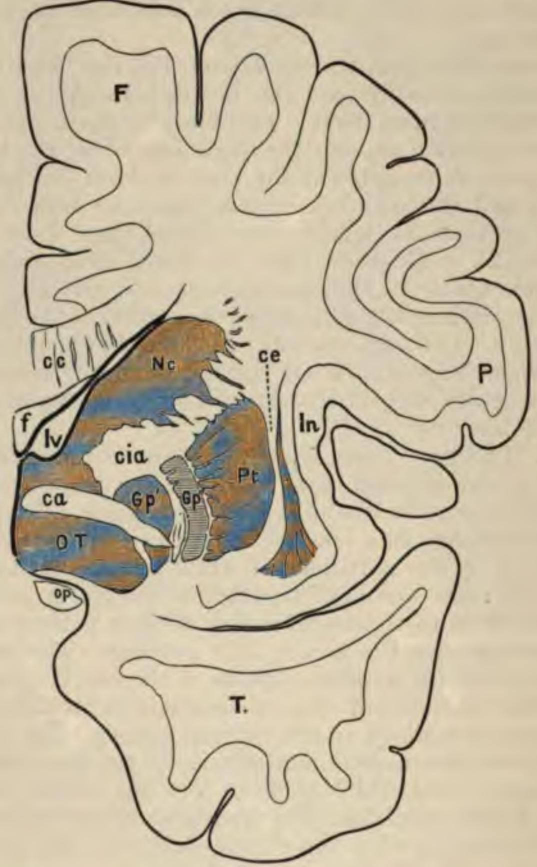

Fig. 121. Diagrammatic Outline of a Transverse Dorsoventral Section through the Right Hemisphere (Man) at a level anterior to Fig. 120. (Natural size.) (Sherrington.)

Nc. nucleus caudatus; *Gp'*, *Gp''*, globus pallidus, seen here in two segments, and *Pt.* putamen of nucleus lenticularis; *OT.* optic thalamus with *ca.* anterior commissure in close relation to *cia.* anterior limb of internal capsule. *ce.* external capsule. *op.* optic tract. *cc.* corpus callosum, *f.* fornix. *lv.* a space that in its upper part belongs to the lateral ventricle, in its lower was filled by the fold of subarachnoid tissue and pia mater, the side fringe of which, covered with epithelium, forms the choroid plexus; this fold was detached in the making of the section and was removed. *In.* the insula; *F.* Frontal lobe; *P.* Parietal lobe; *T.* Temporal lobe.

For greater clearness, the cortical grey matter, which is shaded in Fig. 120, is in this figure left unshaded.

curving so much that the end of the tail sweeping round the hinder border of that body and changing its direction runs eventually ventral to it. In a horizontal section taken at a certain depth such as that represented in Fig. 119 only a portion of the head or body (*Nc.*) in the front part of the figure, and a transverse section of the end of the tail (*Nc.*) in the hind part of the figure are seen; all the intervening portion of the nucleus lies above the plane of the section. In a transverse, dorso-ventral section taken somewhat anteriorly through the front limb of the capsule, Fig. 121, the head or body of the nucleus caudatus (*Nc.*), which has not yet reached its greatest dimensions, is seen lying dorsal to the nucleus lenticularis, separated from it by the white mass of the front limb (*cia*) of the capsule, though this is somewhat broken up by strands of grey matter passing from one nucleus to the

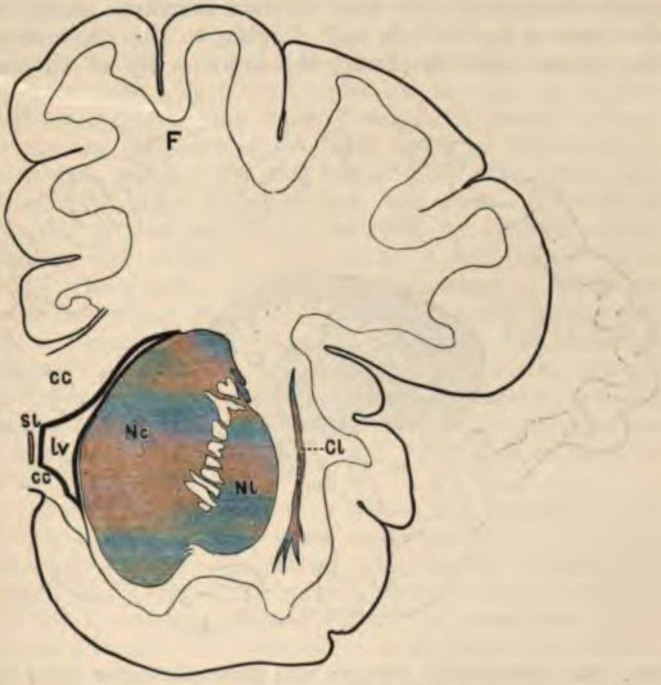

FIG. 122. DIAGRAMMATIC OUTLINE OF A TRANSVERSE DORSOVENTRAL SECTION OF RIGHT HEMISPHERE (MAN) THROUGH THE FRONTAL LOBE. (Natural size.) (Sherrington.)

Nc. Head of nucleus caudatus, and *Nl.* the front end of the putamen of the nucleus lenticularis becoming fused with it. *c. c.* corpus callosum, cut through at its front bend or rostrum so that both dorsal and ventral portions are shewn; between these is seen the fifth ventricle or cavity in the septum lucidum, *Sl.* *lv.* lateral ventricle. *Cl.* claustrum. *F.* Frontal lobe.

Cortical grey matter, as in Fig. 121, left unshaded.

other. In a transverse, dorso-ventral section, taken still more anteriorly, through the frontal lobe (Fig. 122), the head of the nucleus caudatus is seen at about its greatest size, and the diminishing nucleus lenticularis (*Nl.*), represented by the putamen alone, is becoming fused with it, the two nuclei being separated by a small quantity of white matter of the internal capsule and that largely broken up by bridles of grey matter, giving rise to a striated appearance. In a similar section still farther forward, the nucleus lenticularis would be absent, the head of the nucleus caudatus appearing by itself. Returning to the hinder part of the hemisphere, we find in a dorso-ventral section taken through the hind limb of the capsule, Fig. 120, that while the nucleus lenticularis is here at its greatest size, the head of the nucleus caudatus (*Nc.*), lying dorsal to the nucleus lenticularis and separated from it by a considerable thickness of internal capsule, has much diminished; the same section moreover shews, ventral to the nucleus lenticularis and clinging to the descending horn of the lateral ventricle (*l.v.d.*), the extreme tip of the tail of the

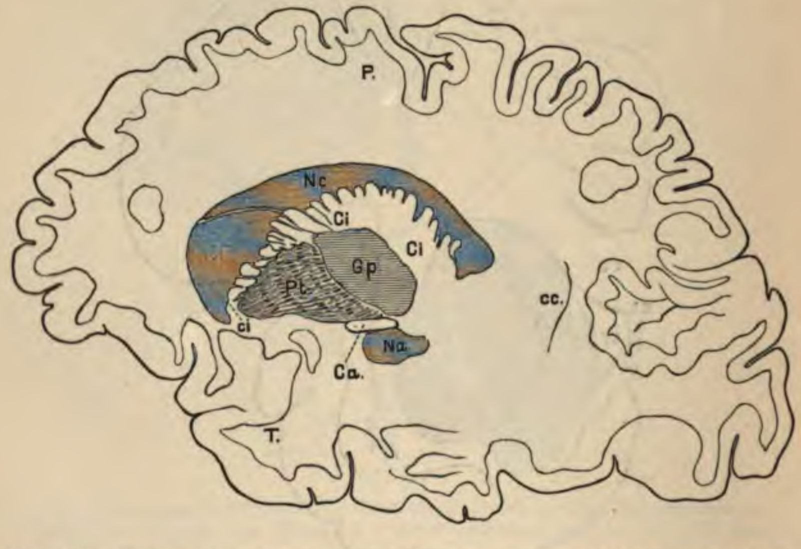

Fig. 123. Diagrammatic Outline of a Sagittal Section taken through the Right Hemisphere (Man) seen from the Mesial Surface. (Half natural size.) (Sherrington.)

The plane of the section is not truly sagittal, but slightly inclined.

Nc. the caudate nucleus exposed, to the left of the letters *Nc.* in nearly its entire anterior extent, to right of the letters in a considerable part of its posterior extent. It forms an arch of grey matter over the grey matter of *Pt.* the putamen and *Gp.* the globus pallidus of the lenticular nucleus. *Na.* the amygdaloid nucleus. *Ci*, *Ci*, *ci*, the internal capsule; *Ca.* the anterior commissure; *cc.* the hinder limit of fibres of the splenium corporis callosi. *P.* the parietal lobe; *T.* the temporal.

nucleus caudatus (*Nc.*) soon about to fuse with the small mass of grey matter called the *nucleus amygdalæ* (*Na.*). A sagittal (longitudinal dorso-ventral) section taken at some distance from the median line (Fig. 123) shews the curved course of the larger portion of the nucleus caudatus, the extreme head as well as the latter part of the tail lying out of the plane of the section; and a similar section taken nearer the middle line (Fig. 126) shews how the nucleus in the middle portion is broken up by bands of fibres of the internal capsule traversing it, and thus contributing to the striated appearance; the same section also shews that the globus pallidus as well as the putamen becomes continuous with the nucleus caudatus.

Thus when we speak of the corpus striatum as a whole we mean a large mass of grey matter lying lateral to the optic thalamus, reaching nearly as far back as that body and stretching much farther forward, as far forward in fact as does the lateral ventricle; but it is important to remember that it is divided into two masses or nuclei, which are fused together and that imperfectly at the very front only. These two nuclei are, the one the comma shaped nucleus caudatus, the bulk of which is placed forward projecting into the lateral ventricle, and which on the whole is the more dorsal portion of the whole body, the other the irregularly shaped nucleus lenticularis, the bulk of which is placed farther back than the lateral ventricle, by the side of the optic thalamus, and which on the whole is the more ventral portion of the whole body. It is no less important to remember that the radiating fibres, which we call the internal capsule, pass in the hinder region of the whole body between the thalamus and the nucleus lenticularis, forming the hind limb of the capsule, and in the front region between the nucleus caudatus and the nucleus lenticularis, forming the front limb of the capsule, the front and hind limbs being bent on each other so as to form an angle, the so-called knee.

§ 628. The optic thalamus as a whole is a somewhat oval mass of grey matter, lying as we have said athwart the diverging crus, in which it is partly imbedded. Its curved median side covered with a thin layer of central grey matter forms the lateral wall of the third ventricle (Figs. 119, 120, 125), and in a longitudinal vertical section of the brain taken in the line of the middle of the third ventricle (Fig. 124, *O.T.*) is seen occupying the space between the fornix and hind end (splenium) of the corpus callosum above, and the diverging crus below. Its more or less straight lateral border abuts on the internal capsule (Figs. 119, 120, 125). Its dorsal surface, as we have already seen, also forms part of the wall of the third ventricle and is free; but there lies close above it the prolongation of the pia mater, forming the velum interpositum with its choroid plexus (§ 602), which creeps in over it beneath the projecting hind end of the corpus callosum and

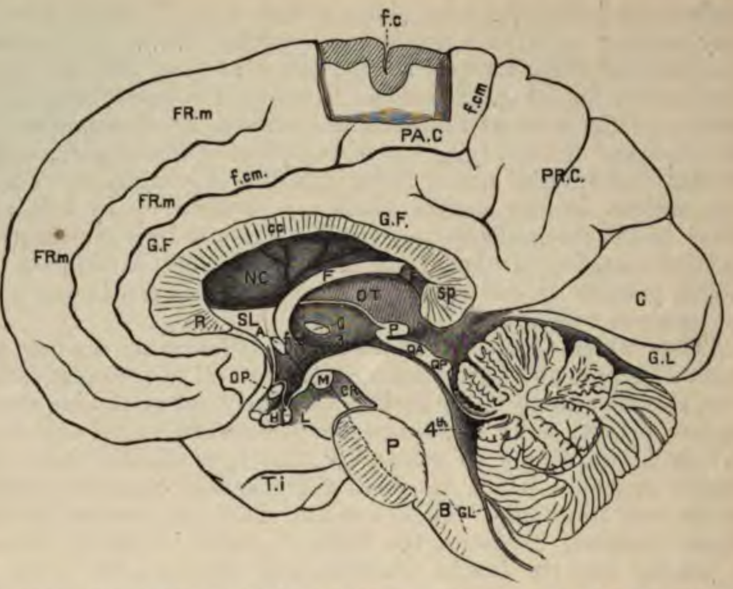

Fig. 124. View of Right Half of Brain of Man, as disclosed by a Longitudinal Section in the Median Line through the Longitudinal Fissure. (Half natural size.) (Sherrington.)

The *bulb*, seen in longitudinal section at *B*, passes into the *pons P*, and into the *crus cerebri*, which last is cut obliquely across as it diverges into the hemisphere and passes out of the section. A part of the ventral surface of the crus is shewn in the shaded part marked *C. R.* At *GL* the *central canal* of the spinal cord is seen opening out into the *fourth* ventricle (4th) overhung by the cerebellum (bisected in the middle line), and passing on by the *aqueduct* beneath the *posterior*, *Q.P*, and *anterior*, *Q.A*, *corpora quadrigemina* into the *third ventricle* (3). The posterior corpus quadrigeminum is continuous behind with the *valve of Vieussens*, attached to the superior peduncle of the cerebellum, and seen in a longitudinal section overhanging the front part of the fourth ventricle. The corpora quadrigemina appear relatively small because the section passes in the median line in the depression between the right and left bodies of the two pairs; and immediately in front of them is the section of the mesially placed *pineal gland P*, which overhangs the opening of the aqueduct into the third ventricle, and the right arm of which running in the lateral wall of the third ventricle is shewn by an unshaded tract.

The roof of the third ventricle is seen to be furnished by the arch of the *fornix F*, shewn unshaded in longitudinal section. Posteriorly the body of the fornix passes into the diverging right *posterior pillar*, where *F* is shaded, and is lost to view under the overhanging rounded hind end or *splenium Sp.* of the *corpus callosum.* In front the body of the fornix is seen passing just behind the transverse section of the *anterior commissure A*, into the diverging right *anterior pillar*, *f*, which is lost to view as it stretches in the lateral wall of the ventricle towards the *corpus mammillare* or *albicans M.* The small white cross immediately behind *f* indicates the position of the *foramen* of *Monro*. The bulging median surface of the *optic thalamus*, *O.T*, is seen forming the lateral wall of the hinder (and, owing to the cranial flexure, the more dorsal) part of the third ventricle, and on this below the area of the pineal gland is seen, unshaded, the section of the *soft* or *middle commissure C.* Between the pineal gland (*P*) and the splenium *Sp*, is seen the hind end or *pulvinar* of the thalamus projecting into the so-called transverse fissure of the brain, shewn shaded in the figure, by which the pia mater passing on beneath the posterior part of the cerebrum and above the cerebellum gains access to the third ventricle, the position of the *velum* being shewn by the thin black line stretching from the splenium to the fornix. The front (and more ventral) part of the third ventricle is seen to end in the *infundibulum* attached to which is the *pituitary body H*, seen in section at *L*. In front of the infundibulum is seen the *optic nerve* cut across at the *optic decussation OP*, stretching from which to the anterior commissure is the *lamina terminalis*.

Stretching between the corpus callosum *c.c.* (seen in longitudinal section with a striated appearance and ending in front at the *rostrum R.* and behind at the splenium *Sp.*) dorsally and the fornix ventrally is seen (unshaded) the *septum lucidum S.L*, but the greater part of this has been cut away in order to disclose the right lateral ventricle in the wall of which is seen the bulging *nucleus caudatus N.C.*

Above the corpus callosum is seen the mesial surface of the right hemisphere forming the right lateral wall of the longitudinal fissure. On this mesial surface appears immediately above the corpus callosum the arched *gyrus fornicatus G.F*, defined above by the *calloso-marginal fissure f.cm.* The whole of the surface seen in the frontal region in front of the calloso-marginal fissure, though divided by fissures, is called the *marginal convolution*. In the middle parietal region a block of the cerebral substance has been removed in order to shew the position of the *central fissure* or *fissure of Rolando*, *f.c.*, and immediately below this is seen a part of *PA.C*, the *paracentral lobule*. In the occipital region *PR.C.* is the *precuneus* or *quadrate lobule*, and *C*, the *cuneus*, while at *G.L* is seen a part of the *lingual lobule*. *T.i* is a part of the *inferior temporo-occipital convolution*, the greater part of which is hidden to view by the pons and crus.

the fornix (Fig. 124). Its ventral surface is fused with the crus; indeed the tegmental or dorsal portion of the crus may be said to end in it and in certain structures lying ventral to the thalamus, in what is called the "subthalamic region" (Fig. 120), while the fibres of the pes pass first ventral and then lateral to it to form the internal capsule.

The grey matter of the whole body is more or less distinctly divided by sheets of white matter, as seen both in horizontal and in vertical sections (Figs. 119, 120, 125), into three parts, which have received the name of nuclei, namely, the *median* or *inner nucleus* (Fig. 120, *in.*), which with the thin layer of central grey matter forms the side wall of the third ventricle, the larger *lateral nucleus* (*ln.*) which abuts upon the internal capsule, and the small *anterior nucleus* (*an.*) which lies on the dorsal surface of the front part of the body and which thus at its front end appears to project into the lateral ventricle.

These three nuclei form however not the whole of the optic thalamus, but only the larger front portion; behind them lies the important portion called the *pulvinar*, into which the hind part of the median nucleus merges; this is partly imbedded in the crus ventrally and in the hemisphere laterally, and is partly free, coming to the surface beneath the hind end of the corpus callosum. In a median longitudinal section of the brain (Fig. 124) it is the pulvinar which forms the cushion-like (hence the name) end of the thalamus beneath the overhanging splenium of the corpus callosum, by the side of the pineal gland; and in the horizontal view (Fig. 119, *Pvr.*), in which the hemispheres are supposed to have been removed, the same pulvinar is seen projecting over the crus by the side of the anterior corpus quadrigeminum. The buried portion of the pulvinar is exposed in a transverse section taken through the anterior corpus quadrigeminum, Fig. 118; the extreme end of this part of the pulvinar (*Pvr.*) is here seen lying dorsal and lateral to the pes of the crus, immediately above two masses of grey matter, the corpora geniculata (*Cgl. Cgm.*), of which we shall speak latter on. One of these, the *lateral* corpus geniculatum (*C.g.l.*), is especially connected with the optic tract (*op.*), and, as we shall see hereafter, the pulvinar itself is also connected with the optic tract and is an important part of the central apparatus of vision.

§ **629**. *The substantia nigra, the red nucleus and other grey matter of the tegmentum.* Nerve-cells and groups of nerve-cells, or areas of grey matter, too small to deserve special names, are scattered throughout the tegmentum along its course. But, besides these and the nuclei of the third and fourth cranial nerves, of which we have already spoken, certain larger collections of grey matter deserve attention. A conspicuous mass of grey matter, circular in transverse section, placed in the midst of the tegmentum on each side but somewhat near the middle line, and stretching from the hinder margin of the third ventricle beneath the anterior corpus quadrigeminum (Figs. 118, 119), is, from the red tint it possesses, called the *red nucleus, nucleus* or *locus ruber.* It is traversed by fibres of the third nerve as these make their way ventrally from the nucleus to the surface.

We must consider also as belonging to the tegmentum a large area of grey matter, somewhat lens-shaped in section (Fig. 118, *Sn.*), which lies between the pes and tegmentum, sharply marking off the one from the other. From its dark appearance due to the abundance of black pigment it is called the *substantia nigra* or *locus niger.* It acquires its largest dimensions at about the middle of the length of the crus, coming to an end in front (Fig. 120, *Sn.*) and fading away behind (Fig. 117) as the crus passes beneath the posterior corpora quadrigemina. These two, the red nucleus and the substantia nigra, are perhaps the most important collections of grey matter in the tegmentum, but we may add that at the front of the crus as the substantia nigra comes to an end there is seen in a somewhat similar position ventral to the hind part of the optic thalamus a collection of grey matter called the *corpus subthalamicum* (Fig. 120, *C.sb.*).

At the hinder part of the crus, as it is about to plunge into the pons, while the pes, now decreasing relatively in size, still continues to be ordinary white matter composed of longitudinal bundles of medullated fibres, the tegmentum takes on more and more the structure which in speaking of the bulb we called reticular formation, and which, as we saw, deserves to be considered as a kind of grey matter.

The grey matter of the pons. When the conjoined crura as we trace them backward plunge beneath the pons the longitudinal fibres of the pes of each crus are, as we have said, soon split up into bundles scattered among the transverse fibres belonging to the pons itself. Dorsal to this system of transverse and longitudinal fibres forming the pons proper, between it on the ventral surface and the central grey matter with the posterior corpora quadrigemina on the dorsal surface, is a region which may be called tegmental since it is a continuation of the tegmentum of the crus. In the front part of the pons (Fig. 117), where the posterior corpora quadrigemina still form the dorsal roof of the section, this tegmental area, which is much broken up by certain strands of longitudinal fibres of which we shall speak later on, contains scattered nerve-cells, and is largely composed of reticular formation. In this is placed on each side a group of nerve-cells, the *locus cœruleus* (Fig. 117, *l.c.*), distinct from the group of cells referred to in § 621 as the origin of the descending root of the fifth nerve (V. *d.*), just ventral to which it lies. This acquires larger dimensions farther back, in the front part of the fourth ventricle (Fig. 119, *l.c.*) between the levels represented in Figs. 116 and 117, and is a collection of large spindle-shaped nerve-cells; it has a bluish tint when its black pigment is seen shining through the surrounding more or less transparent material, hence the name.

In the hinder parts of the pons (Figs. 115, 116), where the cerebellum is seen overhanging the open fourth ventricle, the reticular formation of the tegmental area is still more conspicuous. The only special collection of grey matter in this region to which we need call attention is one which, consisting like the olivary body of the bulb (or inferior olive) of a wall of grey matter surrounding and surrounded by white matter, is called the *upper olive* (Figs. 115, 116, *s.o.*).

The ventral part of the pons, or the pons proper, unlike the pes of the crus, contains mixed with the fibres a very considerable quantity of grey matter. This is fairly abundant in the front part of the pons (Fig. 117) below the corpora quadrigemina, but increases even more behind this (Figs. 115, 116). Hence though the pons proper is largely built up of transverse and longitudinal fibres, and though it contains no compact aggregations of grey matter receiving special names, it does contain scattered throughout it a very large quantity of grey matter, far more indeed than is present in the tegmental portion; the grey matter of the pons, that is of the pons proper, must be regarded as forming a very important part of the grey matter of the crural system, and of no little physiological significance.

Behind the pons the crural system is continued into the bulb, with the structure of which we have already dealt.

4. *Other Collections of Grey Matter.*

§ 630. Of these, three deserve chief attention, and may be classed together, though they differ in nature.

The grey matter of the corpora quadrigemina. On each side of and somewhat dorsal to the central grey matter of the aqueduct which, as we have seen, is well developed, especially on the ventral side, collections of grey matter form the chief part of the corpora quadrigemina, both anterior and posterior.

The grey matter of the anterior corpora quadrigemina (Fig. 118, *A. Q. n.*) is more distinctly marked off from, and separated by a wider tract of white matter from the central grey matter of the aqueduct than is that of the posterior corpora quadrigemina (Fig. 117, *nPQ.*); it is moreover of a different nature. Indeed the two pairs of bodies have quite different relations, are of different nature, and perform different functions.

Corpora geniculata. The two optic nerves, as we shall see in detail later on, give rise, through the optic decussation, to the two optic tracts. Each optic tract (Figs. 112, 118, *Op.*) winds round the crus cerebri on its ventral surface to reach the substance of the hemisphere in the region below the optic thalamus, and as it does so is described as dividing into a lateral and median portion. The lateral portion just as it sweeps round the far edge, that is the outer or lateral edge, of the crus bears a rounded swelling (Fig. 112, B and C, *C.gl.*), the *lateral* or *outer corpus geniculatum*, the interior of which consists largely of grey matter (Fig. 118, *Cgl.*). The median portion similarly bears another like swelling occupying a more median position, the *median* or *inner corpus geniculatum* (Fig. 112, A and B, *Cgm.*), the interior of which (Fig. 118, *Cgm.*) also consists of grey matter. It is to be regretted that these two bodies should bear the same name, for they are different in their origin, in their connections, and in their functions. The lateral body is said to be derived from the forebrain, that is from the vesicle of the third ventricle, has definite connections with the retinal optic fibres, and is distinctly concerned in vision; the median body is derived from the midbrain, is not definitely connected with the retinal fibres, and appears to be in no way concerned in vision. We shall however return later on to the connections and probable functions of these bodies.

Corpus dentatum of the cerebellum. In the midst of the mass of white matter which is formed in the interior of the cerebellum by the confluence of the three peduncles, is found (Fig. 115, *CD*) an area of grey matter arranged, like the olivary body of the bulb, as a sharply folded or plaited band in the shape of a flask or bowl. As in the similar olivary body the grey wall of the flask is covered up by and its interior filled up with white matter; the mouth of the flask is, on each side, directed towards the median line; the fibres pass chiefly to the superior peduncle.

There are also other collections of grey matter in the central white matter of the cerebellum, a pair of which, called the "nuclei of the roof," are said to be connected with the median division of the restiform body (see § 618).

The Arrangement of the Fibres of the Brain.

§ **631**. The systems, tracts and bundles of fibres in which the white matter of the brain is arranged, may be distinguished from each other, partly through mere mechanical separation by means of the scalpel, partly by being traced out with the help of the microscope, but, as in the spinal cord, much more fully and completely by differences of development, and by the method of degeneration.

We have seen that a marked feature of the brain is presented by the two crura cerebri which, running forward from the hind parts of the brain, spread out into each cerebral hemisphere. We have also seen that the crus in the wide sense of the word consists of two parts, a dorsal part, the tegmentum, and a ventral part, the pes or crusta, and that these two parts differ very strikingly from each other in structure and in relations. The pes consists exclusively of bundles of longitudinal fibres, and we may trace these from the cerebral hemispheres into the pons and some of them beyond the pons into the bulb and spinal cord. The tegmentum is more complex in structure; it consists of grey matter, and of fibres and bundles of fibres having various relations, both with the collections of grey matter lying within itself and with surrounding structures. It too has connections with the parts lying in front of it, and with the parts lying behind it; we may trace it too backwards through the pons into the bulb and forwards to the optic thalamus. If we allow ourselves to conceive of the optic thalamus as constituting the front ending of the tegmentum, we may arrange a large part of the brain into two main regions, into a tegmental region stretching from the optic thalamus through the dorsal portion of the pons to the dorsal portion of the bulb, and into a region, which we may call the pedal region, stretching from the internal capsule through the ventral portion of the pons to the ventral portion of the bulb.

The fibres of the brain as a whole may be broadly classified into longitudinal tracts connecting parts of the brain with succeeding parts and into transverse or commissural tracts between one lateral half and the other, and into tracts connected with the several cranial nerves. Taking the longitudinal fibres first we may in accordance with the division just explained into a pedal and a tegmental region, consider these as forming on the one hand a pedal, and on the other hand a tegmental system.

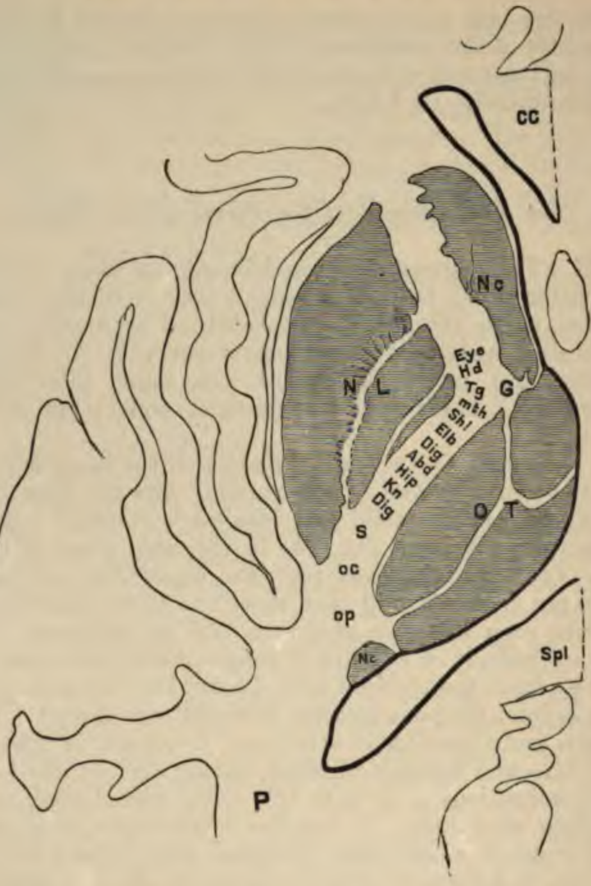

Fig. 125. Outline of Horizontal section of Brain, to shew the internal capsule. (Natural size.)

The section is taken at a level more ventral than shewn in Fig. 119. The grey matter of the cortex and claustrum is left unshaded, but that of the corpus striatum and optic thalamus is shaded.

OT. optic thalamus, shewing the median, lateral, and anterior nuclei. *NL.* nucleus lenticularis, showing the putamen large, and the inner division of the globus pallidus very small. *NC.* nucleus caudatus, the large head in front of, and the diminishing tail behind, the thalamus.

G. the knee of the internal capsule. From '*Eye*' to '*Dig.*' marks the position of the pyramidal tract as a whole, and the several letters indicate broadly the relative positions of the several constituents of the tract, named according to the movements with which they are concerned; thus *Eye* movements of the eyes; *Hd.* of the head; *Tg.* of the tongue; *mth.* of the mouth; *Shl.* of the shoulder; *Elb.* of the elbow; *Dig.* of the hand; *Abd.* of the abdomen; *Hip*, of the hip; *Kn.* of the knee; *Dig.* of the foot.

S. the temporo-occipital tract. *oc.* fibres to the occipital lobe. *op.* optic radiation. At this level the fibres of the frontal tract, in the fore limb of the capsule in front of the pyramidal tract, run almost horizontally, parallel with the plane of the section. Cf. Fig. 122, *Fron.*

cc. the rostrum of the corpus callosum, *Spl.* the splenium of the same, both cut across horizontally. The thick dark line indicates the boundary of the cavities of the anterior and descending horns of the lateral ventricle and of the third ventricle, the two ventricles being laid open into one by the removal of the velum and choroid plexus &c. The oval outline in the fore part of this cavity indicates the fornix.

Lateral to the nucleus lenticularis is seen in outline the claustrum, the cortex of the island of Reil and the operculum or convolution overlapping the island of Reil.

P is inserted to shew which is the hind part of the section.

Both systems begin, as we shall see, in the cortex of the cerebral hemispheres. We shall have to deal with the topography of the cortex later on, but may here say that the first broad division of the whole surface of a hemisphere is into four main regions: frontal, parietal, occipital and temporal (Figs. 120, 121, 125).

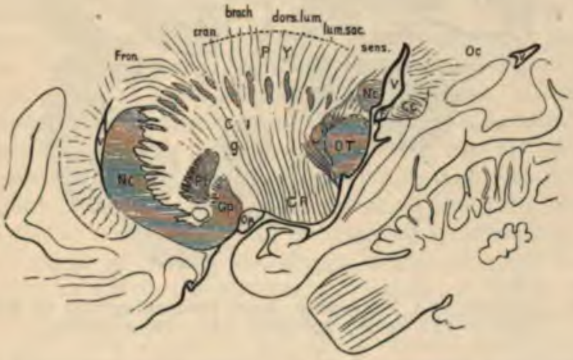

FIG. 126. OUTLINE OF A SAGITTAL SECTION THROUGH THE HEMISPHERE. Man. (Sherrington.)

The section is taken not far to the right of the median plane and is one half linear of natural size. The grey matter of the corpus striatum and thalamus is shaded.

Nc. Nc. the caudate nucleus; *Pt.* the putamen and *Gp.* the globus pallidus of the lenticular nucleus; *OT.* the optic thalamus; *CI.* the internal capsule, with a streaked appearance revealing approximately the direction taken by fibre-bundles passing into it from the portion of corona radiata over it. In these sets of bundles may be broadly distinguished a frontal system, *fron.* a pyramidal system, *P Y* (sub-divisible into cranial (*cran.*), brachial (*brach.*), dorso-lumbar (*dors. lum.*), and lumbo-sacral (*lum. sac.*) parts) and a temporo-occipital system, *sens.*; the situation of the genu of the internal capsule is indicated by *g*. *C R* the crus cerebri; *Oc.* the so-called optic radiations passing into the occipital lobe; *cc.* the splenial end of the corpus callosum; *v, v, v,* the lateral ventricle cut across in three different places; *F.* the fornix in cross-section; *Op.* the optic tract in cross-section. Part of the cerebellum is seen in outline to the right.

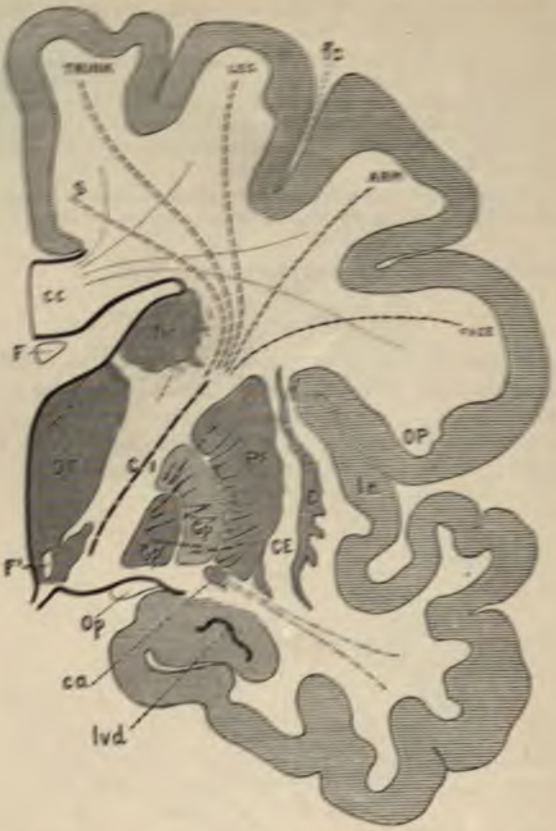

FIG. 127. OUTLINE OF A TRANSVERSE DORSO-VENTRAL SECTION OF THE RIGHT HALF OF THE BRAIN. (Natural size.) (Sherrington.)

The section which is taken at the level of the knee of the capsule, and is therefore intermediate between those shewn in Figs. 120, 121, is introduced to illustrate the course of the constituents of the pyramidal tract.

O.T. optic thalamus; *N.c.* nucleus caudatus, the head only appears in this section. *Pt.* putamen, *Gp''*. *Gp'*. the two parts of the globus pallidus of the nucleus lenticularis; *C.* the claustrum; *C.E.* the external capsule; *In.* the island of Reil. *c.a.* the anterior commissure, shaded to render it distinct, and the fibres from the temporo-sphenoidal lobe which pass into it being indicated by broken lines. *Op.* the optic tract; *lvd.* the end of the descending horn of the lateral ventricle; *F.* the fornix; *F'.* the end of the anterior pillar of the fornix in the base of the thalamus; *c.c.* corpus callosum; *OP.* anterior part of the occipital lobe.

f.c. is the central fissure or fissure of Rolando. The course of the fibres of the pyramidal tract connected respectively with the trunk, leg and arm, and hence with spinal nerves, and of those connected with the face, and hence with cranial nerves, is shewn by broken lines. These are all seen converging into the internal capsule *C.I.* This figure should in respect to the course of these fibres be compared with the horizontal section shewn in Fig. 121, and the sagittal figure shewn in Fig. 126.

S. indicates the course of the most anterior and dorsal part of the temporo-occipital tract.

The fine dotted lines converging to the corpus callosum *c.c.* indicate the course of the callosal fibres.

Longitudinal Fibres of the Pedal System.

§ **632.** *The pyramidal tract.* We have already (§ 575) said that the pyramidal tract of the spinal cord may be traced to a particular region of the cerebral cortex. We shall study the details of this region, which is often spoken of as the "motor area," later on, but may here say that broadly speaking it is parietal in position and corresponds to the parts of the cortex gathered round the fissure of Rolando. Fibres passing from the grey matter of the cortex of this region to the white matter below, and so contributing their share to the central white matter of the hemisphere, converge (Figs. 126, 127) to form part of the internal capsule, namely that part which in a horizontal section (Fig. 125, *Eye* to *Dig.*) occupies the knee and stretches for more than half, or nearly two-thirds, along the hind limb of the capsule, between the optic thalamus on the inside and the nucleus lenticularis on the outside. From the knee and hind limb of the capsule they pass by the side of and ventral to the optic thalamus (Figs. 120, 127), and so contribute to form the beginning of the crus cerebri. In thus converging to take up their position in the capsule and in their further passage to the crus the fibres follow a course of somewhat complicated curvature. As we trace the capsule from more dorsal to more ventral levels, we find it continually changing in form; the exact shape of the capsule shewn in Fig. 125 only holds good for the level at which the section was taken; it differs somewhat from that shewn in Fig. 119 taken at a slightly different level, and sections still more dorsal or still more ventral would present still greater differences. When we examine a series of horizontal sections, taken in succession from the dorsal to the ventral regions, we find that the knee shifts its position and changes in the width of its angle, that the two limbs vary in direction in size and in shape, and that at last the bent flattened capsule passes into the more or less rounded crus by the rapid disappearance of the fore limb, and the consequent extinction of the angle; so that in one sense it is the hind limb which becomes the crus, and the fibres of the fore limb may be said to pass into the crus through the ventral portion of the hind limb. Hence it is obvious that the fibres of the pyramidal tract, like the other fibres of the capsule, are continually changing their direction as they pass through the capsule. Moreover while the fibres from different parts of the 'motor area' assume definite positions in relation to each other as they pass into the capsule, their relative positions are not constant, but vary somewhat. To this point however we shall return when we come to speak of the function of this tract.

In the crus these fibres run exclusively in the pes and form a compact strand (Fig. 118, *Py*) occupying the central and larger portion of the pes between a small median portion on the inside and a lateral portion on the outside. Maintaining this position along the crus they enter the pons, but here the previously compact strand is split up, by the interlacing transverse fibres of the pons, into a number of scattered bundles, which however as a whole still keep their central position. They form the greater part of but not all the bundles seen cut transversely in transverse sections of the pons (Figs. 116, 117). Farther backwards they become the pyramid of the bulb, and so give rise in the spinal cord to the direct and crossed pyramidal tracts. These fibres from the motor area of the cortex of the cerebrum are thus the source of the pyramidal tracts of the spinal cord, and hence the whole strand of fibres from the cortex downwards has been called the pyramidal tract. We have said (§ 575) that we have reasons for thinking that the pyramidal tract in the spinal cord makes connections through the grey matter of the ventral horn with the ventral roots of all the spinal nerves in succession; and similarly we have reason to think that along its course in the crus, in the pons, and in the bulb, before it reaches the cord, the tract also makes connections with the nuclei of those cranial nerves which are motor in function. During the passage of the tract through the internal capsule the fibres destined for cranial nuclei occupy the knee, while those belonging to the spinal cord run in the hind limb. Some authors limit the term pyramidal tract to the spinal moiety, since this alone forms the pyramid; but this is undesirable.

This tract is well marked out by the degeneration method, and the degeneration in it is a descending one, the trophic centres of the fibres being cells in the grey matter of the cortex. Removal of or injury to the cortex of the whole motor area gives rise to a degeneration along the whole tract, and removal of or injury to part of the area gives rise to degeneration of some of the strands. The tract is also well marked out by the embryological method; the fibres belonging to it acquire their medulla at times later than those of any other fibres.

Anterior or frontal cortical. Fibres from the grey matter of the cortex in front of the motor area also pass to the internal capsule, but occupy the fore limb (Fig. 126, *fron*). Thence they pass to the crus, of which they form the small inner, median portion of the pes (Fig. 118, *Fr.*), and from the crus pass into the pons; in transverse sections of the pons they are seen as scattered bundles (Fig. 117, *F.C.*) to the median side of the pyramidal fibres. But here they seem to end; the degeneration of the tract is a descending one, and ceases here. Most probably the fibres end in the nerve-cells of the grey matter, which, as we have seen, is abundant in the pons. It is also probable that through these nerve-cells the fibres of this tract are connected with transverse fibres passing along the middle cerebellar peduncle into the cerebellum of the opposite side; but this has not been definitely proved.

Posterior or temporo-occipital cortical. Fibres from the grey matter of parts of the cortex behind the motor area also converge to the internal capsule, forming the hinder end of the hind limb behind the pyramidal tract (Fig. 125, *S*). These fibres also contribute to form the crus cerebri, passing into the pes, of which they occupy the outer lateral portion (Fig. 118, *Pr. O.*). From the crus they pass into the pons, where, like the fibres of the preceding tract, they appear to end, and probably in a like manner. This tract has been described as one of ascending degeneration, but in all probability like the preceding is one of descending degeneration.

The above three tracts of fibres may therefore all be regarded as starting from or having their trophic centres in the cortical grey matter of the hemispheres, as all helping to form, first the internal capsule and then the pes of the crus cerebri. But while the pyramidal tract passes, in part, to the spinal cord, the other two cease at the pons, and probably through the grey matter of the pons make connections with the cerebellum. Further, while the pyramidal tract coming from the middle region of the cortex occupies a middle position in the capsule and a middle position in the crus, the system from the front part of the cortex occupies a front position in the capsule and an inner or median position in the crus, and the system from the hind part of the cortex a hind position in the capsule and an outer or lateral position in the crus. As the three systems pass from the cortex through the capsule to form the pes of the crus, their positions in relation to each other are shifted from one plane into another. As the fibres spread out from the pes through the capsule to all parts of the cortex, or, put in another way, as they converge from the cortex through the capsule to the pes, they form a fan, the corona radiata, which is not only curved, but the constituent parts of which cross each other.

Besides these three systems all passing from various regions of the cortex to the crus, there is yet a fourth strand contributed to the pes by the cerebral hemisphere though not starting in the cortex. *From the nucleus caudatus* fibres pass down to the crus, and take up a position in the pes dorsal to the tracts just mentioned, occupying a lens-shaped area immediately ventral to the substantia nigra, and probably passing into the substantia nigra itself. These cannot be traced farther down than the pons, where they appear to end, though possibly some terminate higher up in the substantia nigra. This tract has a descending degeneration, and may be regarded as a tract analogous to the front and hind cortical tracts, though it begins not in the cortex but in the nucleus caudatus; it is not however a very pure tract, many fibres of the pyramidal tract passing into it in the pes.

These are the main tracts of the pedal system. For, though the nucleus lenticularis gives off fibres to the internal capsule, our knowledge of the further course of these is at present imperfect, and though there seem to be longitudinal fibres connecting the bulb, the pons, and the pes at various levels, these are not numerous, and at all events do not form conspicuous strands.

Longitudinal Fibres of the Tegmental System.

§ **633**. *Cortical fibres.* Although the fibres of the pedal system form, as we have seen, the greater part of, they do not form the whole of, the internal capsule. Fibres coming from or going to all or nearly all parts of the cortex, though they help to form the internal capsule, do not go on to form the pes, but pass to the optic thalamus (Fig. 120, *l.l.*) and appear to end in the grey matter of that body. In their passage through the capsule the fibres of this nature from the frontal and parietal regions of the cortex occupy the extreme front end of the front limb in front of the frontal strand of the fibres of the pedal system (Fig. 125, *Th.*). The fibres from the occipital and temporal regions, those from the occipital regions being the most numerous and indeed being very conspicuous, occupy the extreme hind end of the hind limb of the capsule, behind the temporo-occipital division of the pedal system (Fig. 125, *Op.*). Since, as we shall see, we have reason to associate the occipital region of the cortex with vision, the fibres thus radiating to (or from) the thalamus through the extreme hind limb of the capsule from (or to) the occipital cortex have been called the *optic radiations.*

All the fibres of the optic radiations do not however end in the thalamus; some may be traced to the grey matter of the anterior corpus quadrigeminum and of the lateral corpus geniculatum running in the so-called 'brachia' of those bodies.

We may here perhaps diverge for a moment to point out the contrast between the optic thalamus and the corpus striatum, or at least the nucleus caudatus. The former does not contribute to the pedal system, the latter supplies a marked contribution. The former receives fibres from all parts of the cortex; there are no such special contributions from the cortex to the latter. And this difference accords with the experience that when parts of the cortex are removed, or are congenitally absent, no degeneration or want of development is observed in the corpus striatum, while degeneration or want of development is observed in the optic thalamus as well as in parts of the pedal and tegmental systems. Hence, while we may regard the optic thalamus as an intermediate mass of grey matter exchanging fibres with the cortex, and thus connecting the cortex with other hinder parts of the tegmental system, the corpus striatum appears rather to be analogous to the cortex itself, to be a special modification of the cortex, sending fibres down into the pedal system, but itself receiving no special tracts of fibres from the cortex. Indeed we may probably regard the corpus striatum as the oldest part of the superficial grey matter of the hemisphere, the more ordinary cortex being a later development.

The tegmentum, lying ventral to the hind end of, and behind the thalamus, in which region, as we have seen, the conspicuous red nucleus is situated, is thus, by reason of its connection with the thalamus, indirectly connected with the cortex. But besides this, it has direct connections of its own with the cortex. Other fibres from the frontal and parietal regions traversing the lenticular nucleus in the sheets of white matter splitting the nucleus into parts, are also said to reach the tegmentum either by piercing through or by sweeping round the internal capsule. On their path these fibres are, according to some observers, joined by fibres coming from the lenticular nucleus itself, and possibly from the caudate nucleus, which fibres, on the view that these nuclei are modified cortex, may also be considered as cortical. Thus the forepart of the tegmental region is brought into ample connection with the cerebral hemisphere partly by fibres joining the thalamus, partly by fibres passing directly to itself.

The mode of degeneration of these cortical fibres of the tegmental system is at present a matter of dispute. Nor is the general nature of the fibres conclusively determined, though it is generally supposed that they carry impulses from the thalamus and parts of the tegmentum to the cortex.

§ **634**. In the tegmentum from the subthalamic region to the bulb the reticular formation is, as we have seen, more or less abundant; this, and the occurrence of various bundles of fibres, gives the region great complexity; and we must confine ourselves here to touching on one or two important longitudinal strands which traverse it.

The *superior peduncle of the cerebellum* is one of the most important of these. This is on each side a bundle of fibres which, taking origin in part from the grey matter of the nucleus dentatus, and the smaller neighbouring collections of grey matter, but also from the superficial grey matter, leaves the cerebellum in front of, and to the median side of the restiform body and passes forward towards the corpora quadrigemina. At first the two peduncles are superficial and dorsal in position (Figs. 115, 116, *S.P.*) and the space between them is bridged over by the valve of Vieussens (Fig. 116, *Vla*); but, still converging, they soon sink ventrally beneath the posterior corpora quadrigemina and at the level of the junction between the anterior and posterior corpora quadrigemina meet and decussate ventral to those bodies in the ventral region of the tegmentum (Fig. 117, *S.P.*). Beyond the decussation they are continued forwards in the tegmentum ventral to the anterior corpora quadrigemina as two strands, one on each side, which appear to end in the red nuclei.

In this way the peduncles connect certain parts of the grey matter of the cerebellum with the tegmental region, and more particularly with the red nucleus, and thus indirectly with the structures with which that region is itself connected.

The fillet. This, as we have seen (§ 612), takes origin in the bulb, in the interolivary layer between the inferior olives, from fibres which are derived through the supra-pyramidal or sensory decussation from the gracile and cuneate nuclei. From this origin it passes forward on each side as a flat band into the tegmental region of the pons, receiving accessions from the superior olive and other collections of grey matter, and dividing there into two strands, the median (Figs. 116, 117, *Fm.*) and lateral (Figs. 116, 117, *Fl.* and Fig. 112, B *F*) fillet. The lateral division, which receives fibres from the cochlear nucleus, and which as we shall see later on serves apparently as a path for auditory impulses, ends partly in the grey matter of the posterior corpus quadrigeminum, and partly in the white matter underlying (Fig. 118, *dm*) the anterior corpus quadrigeminum. The median division, into which pass sensory fibres from the accessory-vago-glossopharyngeal nucleus, and from the cells belonging to the 'ascending' root of the fifth nerve, and which seems to be a special path for sensory impulses, appears partly to end in the grey matter of the anterior corpus quadrigeminum, but chiefly to be continued on to the subthalamic region of the tegmentum ventral to the thalamus and to end largely in the thalamus itself. It has been stated that some of the fibres pass on beyond the thalamus to end in the cerebral cortex; but it is doubtful whether more than a few thus pass. It is probable that impulses passing along the fillet do reach the cortex, but it is also probable that these undergo a relay in the cells of the thalamus or elsewhere.

The longitudinal posterior bundles. In a transverse section through the fore part of the pons at the level of the posterior corpora quadrigemina a rather conspicuous bundle of longitudinal fibres (called the longitudinal posterior bundle) is seen on each side, cut transversely, in the dorsal region of the tegmentum just ventral to the nucleus of the fourth nerve (Fig. 117, *l.*). Traced backward from the aqueduct beneath the fourth ventricle, it becomes less conspicuous (Fig. 116, *l.*) though maintaining its position dorsal to the reticular formation, and at the hind end of the bulb appears to be a continuation forwards of those fibres, "ground fibres," of the ventral column of the cord which probably serve as successive short longitudinal commissures between the segments of the cord. While the somewhat analogous fillet runs ventral to the reticular formation, this posterior longitudinal bundle runs always dorsal to that structure. It may be traced forward as far as the nucleus of the third nerve, and is seen in transverse sections lying immediately ventral to that group of cells (Fig. 118, *l.*). A considerable portion of the fibres of the longitudinal posterior bundle arise from a nucleus lying a little anterior and dorsal to the nucleus of the third nerve; these are descending fibres, degenerating, when they are divided, below the level of the section. Other fibres, also descending, probably arise from the grey matter behind the above nucleus. The bundle also receives fibres spoken of as ascending fibres, from cells of the reticulate formation and of the various sensory nuclei of the spinal bulb, especially it is said from the nucleus of the vestibular nerve; and some of the fibres are said to come from the grey matter of the anterior corpus quadrigeminum. The fibres of the bundle, by their terminals or collaterals, form synapses with the cells of the nuclei of the oculo-motor and probably of the other motor cranial nerves; they thus afford a mechanism for bringing afferent and efferent fibres into direct connection. The bundle is relatively more prominent in the lower than in the higher animals, and its fibres acquire their medulla relatively early.

Tracts from the corpora quadrigemina. From each corpus quadrigeminum there passes obliquely forwards and downwards on each side a band of fibres, connected with the grey matter of the corpus and known as its *brachium*. The anterior brachium (Fig. 118, *Ba*), as we shall see in dealing with the optic nerve, joins the lateral corpus geniculatum and helps to form the optic tract, but some of its deeper lying fibres proceed to the occipital cortex forming part of the fibres which we have (§ 633) described as passing from the occipital cortex to and past the thalamus. The posterior brachium passes to the median corpus geniculatum; having received fibres from, and probably given fibres up to that body, it is continued on to the tegmentum, and according to some authors through the tegmentum by the hind part of the hind limb of the internal capsule to the temporal region of the cortex, mingling in its course with fibres from the thalamus.

Transverse or so-called Commissural Fibres.

§ **635.** The two chief masses are those on the one hand belonging to the cerebrum, and those on the other hand belonging to the cerebellum.

In the cerebrum the most imposing mass of transverse fibres forms the *corpus callosum*. Starting from the cortex in nearly all parts of the hemisphere, the fibres, which are largely if not wholly collaterals of axons descending from cells in the cortex, converge towards the thick body of the corpus callosum placed in the middle line, and thence diverge to nearly all parts of the cortex of the hemisphere on the other side, interlacing in their course with the cortical fibres of the pedal and tegmental systems. By means of these fibres parts of the cortex of one hemisphere are brought into connection with parts of the cortex of the other hemisphere.

Besides these callosal fibres from one hemisphere to another, the white matter of each hemisphere contains fibres called "association fibres," passing from one convolution to another of the same hemisphere.

The small *anterior white commissure* though it is placed in the front part of the third ventricle (Fig. 124, *A*) and, in part of its course, lies along the thalamus (Fig. 121, *Ca*) is really a commissure of particular parts of the cerebral hemispheres. A portion, very small in man, belongs to the olfactory tract; the rest takes origin on each side in a limited portion of the cortex (Fig. 120, *Ca*), which we shall later on speak of as the temporo-sphenoidal convolution and in which callosal fibres are deficient, whence it arches forward through the globus pallidus, past the thalamus (Figs. 127, *ca*, 121, *Ca*) to the front part of the third ventricle. It may be remarked that this commissure is particularly large in animals specially endowed with the sense of smell, and is still found in those lower animals which do not possess an obvious corpus callosum.

The small posterior commissure may be regarded as mainly a commissure between the two thalami, but it also helps to unite the tegmentum of the two sides, and some fibres are said to pass on each side into the hemisphere. The middle or soft commissure of the third ventricle (Fig. 119, *c*), though it contains transverse fibres, is in the main a collection of grey matter, indeed a part of the central grey matter.

The *fornix*, together with, at all events, part of the septum lucidum which joins it with the corpus callosum, must also be regarded as a commissural structure. But its relations are peculiar; for while, behind, the diverging posterior pillars begin in the cerebral hemispheres, namely, in the walls of the descending horn, cornu ammonis, of the lateral ventricle on each side, in front the anterior pillars or columns, leaving the cerebral hemispheres, pass along the lateral walls of the third ventricle (Fig. 124, *f*), and may be traced to the corpora albicantia; from thence they are said to pass, decussating, to the tegmentum. From each corpus albicans the bundle of fibres known as Vicq d'Azyr's bundle (Fig. 120, *Vb*) passes to the tegmentum, running in the lateral wall of the third ventricle. The fibres of the fornix are stated to be the axons of cells in the cornu ammonis, while those of Vicq d'Azyr's bundle are axons of cells in the corpus albicans.

In the cerebellum transverse though not true commissural fibres are supplied by the *middle peduncles*. In contrast to the fibres of the superior peduncle which start from the nucleus dentatus, and other internal grey matter, as well as from the superficial grey matter, and to those of the inferior peduncle which start from or end in chiefly the superficial grey matter of the vermis, the fibres of the middle peduncle appear to start exclusively from the superficial grey matter but from that of the whole surface, from that of the median vermis as well as from that of the lateral hemispheres; they thus form the greater part of the central white matter. Sweeping down into the pons, they form the transverse fibres of that body, interlacing with the longitudinal fibres of the pedal system. They cross from one side of the cerebellum to the opposite side of the pons, and end in the grey matter there so abundant. They do not pass into the opposite peduncle and so to the surface of the opposite cerebellar hemisphere. Hence, as we have said, though transverse fibres, they are not true commissural fibres; the few truly commissural fibres of the cerebellum are to be found in the white matter of the vermis.

Some, indeed the majority, of these fibres of the middle peduncle are axons of cells (of which we shall speak later on) in the superficial grey matter of the cerebellum and end in connection with the cells of the grey matter of the pons; others are axons of cells of the grey matter of the pons and end in the superficial grey matter of the cerebellum. The former probably carry impulses from the cerebellum to the pons, the latter from the pons to the cerebellum; in both cases the impulses cross from one side to the other. The fibres of the pedal system either by terminals or collaterals connected with the same grey matter of the pons, but on the same side. Thus through the intervention of the grey matter of the pons a connection is supplied between a cerebral hemisphere and the crossed hemisphere of the cerebellum.

It is further supposed that other fibres of the middle peduncle reaching the pons do not cross the median line, but keeping to the same side and changing their direction, take a longitudinal upward course either with or without the intervention of nerve-cells, and so make their way to the tegmentum. But this is not certain.

We must also consider as commissural structures the numerous fibres crossing, or serving to form the median raphe in the bulb. This raphe, with similar commissural fibres, is present in the tegmental portion of the pons, and indeed in the tegmentum itself.

Fibres also cross from one side to the other in connection with the cranial nerves, but these as well as all the tracts specially connected with the cranial nerves, including the olfactory and optic nerves, had better be considered by themselves.

Summary.

§ 636. It may perhaps appear from the foregoing that the brain consists of a number of isolated masses of grey matter, some large, some small, connected together by a multitude of ties of white matter arranged in perplexing intricacy; and the addition of numerous collections of grey matter and strands of white matter of which we have made no mention would still further increase the perplexity. Nevertheless a systematic arrangement may be recognized, at least to a certain extent.

The least conspicuous, but perhaps in point of origin the oldest part of the brain, seems to be what we have called the central grey matter. This seems to serve chiefly as a bed for the development of the nuclei of the cranial nerves.

Next to the central grey matter and more or less associated with it comes what we have called the tegmental region, of which the reticular formation, coming into prominence in the bulb and continued on to the subthalamic region, forms as it were the core. Belonging to the tegmental system are numerous masses of grey matter from the conspicuous optic thalamus and the red nucleus in front to the several nuclei of the bulb behind. This complex tegmental system, which may perhaps be regarded as a more or less continuous column of grey matter, comparable to the grey matter of the spinal cord, serves as a sort of backbone to the rest of the central nervous system. With the spinal cord it is connected by various ties, besides being as it were a continuation of the spinal grey matter, and around it are built up the great mass of the cerebrum, and the smaller but still large mass of the cerebellum; the less important corpora quadrigemina we may for simplicity's sake neglect.

At the hind end we find various parts of the spinal cord becoming connected with this tegmental system, either passing into it and becoming, as far as our present knowledge goes, lost in it, or supplying strands or fibres which passing into it become through it connected with other parts. Thus the ventral column of the cord exclusive of the direct pyramidal tract, the lateral column exclusive of the crossed pyramidal and cerebellar tracts (and the antero-lateral ascending tract), together with part of the dorsal column appear to join the tegmental system, while part of the dorsal column, after the relay of the gracile and cuneate nuclei, passes through the system as the fillet destined for various structures.

At the front end we find all parts of the cerebral cortex (though some regions, namely, the temporo-occipital, to a greater extent than others) connected with the thalamus and other parts of the tegmental system; and, as we have seen, the corpus striatum may possibly possess like connections.

The relations of the cerebellum to this system are notable. On the one hand the cerebellum is directly connected with the system, partly by fibres which pass from the bulb to join the restiform body or inferior peduncle, and partly by the superior peduncles which, as we have seen, are in a measure lost in the tegmentum. On the other hand the cerebellum forms around the tegmental system a great junction between the spinal cord and the cerebrum. To the spinal cord it is joined in a direct manner by the cerebellar tract and by the antero-lateral ascending tract, and in an indirect manner by the relay of the gracile and cuneate nuclei. To all parts of the cerebral cortex, it appears to be joined by those conspicuous strands of the pedal system, which, as we have seen, end in the pons, and there make connections with the fibres of the middle peduncle. And we may here perhaps remark that while this connection between the cerebrum and cerebellum is wholly a crossed one, each cerebral hemisphere being joined with the opposite half of the cerebellum, the connections between the spinal cord and the cerebellum are largely uncrossed ones, that by the cerebellar tract being wholly uncrossed, and that with the posterior column by the relay of the gracile and cuneate nuclei being in part uncrossed.

Thus the cerebral cortex has a double hold, so to speak, on the rest of the central nervous system, first through the tegmental system, and secondly through the cerebellar junction. But in addition to this there is another tie between the cerebral cortex and the whole length of the cerebro-spinal axis, or at least between it and the whole series of motor mechanisms in succession from the nucleus of the third nerve to the nucleus, if we may so call it, of the ventral root of the coccygeal nerve, namely, the great pyramidal tract, which thus appears (in mammals) as a something superadded to all the rest of the central nervous system.

When the cerebral hemispheres are removed this pyramidal tract falls away, as does also the pedal system leading from the cerebrum to the pons, but there still remains the tegmental system with its cerebellar and other adjuncts, and this, as we shall see, constitutes a nervous machinery, capable of carrying out exceedingly complicated acts.

SEC. 4. ON THE PHENOMENA EXHIBITED BY AN ANIMAL DEPRIVED OF ITS CEREBRAL HEMISPHERES.

§ **637.** The cerebral hemispheres, as we have more than once insisted, seem to stand apart from the rest of the brain. In the case of some animals it is possible to remove the cerebral hemispheres and to keep the animal not only alive, but in good health for a long time, days, weeks, or even months after the operation. In such case we are able to study the behaviour of an animal possessing no cerebral hemispheres and to compare it with that of an intact animal. Such an experiment is most readily carried out on a frog. In this animal it is comparatively easy to remove the cerebral hemispheres, including the parts corresponding to the corpora striata, leaving behind intact and uninjured the optic thalami with the optic nerves, the optic lobes (or representatives of the corpora quadrigemina), the small cerebellum and the bulb. If the animal be carefully fed and attended to, it may be kept alive for a very long time, for more than a year for instance.

The salient fact about a frog lacking the cerebral hemispheres, is that, as in the case of a frog deprived of its whole brain, the signs of the working of an intelligent volition seem to be, at first at least, wholly absent. The presence of the bulb and the middle parts of the brain (for so we may conveniently call the cerebral structures lying between the cerebral hemispheres and the bulb) ensures the healthy action of the vascular, respiratory and other nutritive systems; food placed in the mouth is readily and easily swallowed; the animal when stimulated executes various movements; but if it be left entirely to itself, and care be taken to shield it from adventitious stimuli, either it remains perfectly and permanently quiescent, or the apparently spontaneous movements which it carries out are so few and so limited as to make it very doubtful whether they can fairly be called volitional. Such a frog, for instance, after being kept alive for some time and made to exhibit the phenomena of which we are about to speak, has been placed on a table with a line drawn in chalk around the area covered by its body, and left to itself has subsequently been found dead without having stirred outside the chalked line.

We must here however repeat the caution laid down in § 582, as to the ultimate effects of an operation on the central nervous system. The longer the frog is kept alive and in good health after the removal of the cerebral hemispheres, the greater is the tendency for varied and apparently spontaneous movements to shew themselves. For days or even weeks after the operation there may be no signs whatever of the working of any volition; but after the lapse of months, movements, previously absent, of such a character as to suggest that they ought to be called voluntary, may make their appearance. These become especially marked, if the animal, well fed and well cared for, instead of being kept amid the artificial conditions of a laboratory, is placed in circumstances as natural as possible and thus subjected to the various influences which determine the usual life of a frog. If for instance it have free access to land and water it will move from the land to the water and back again; at the approach of winter it will bury itself for hybernation and on the return of spring will come forth again; and in some instances it has been seen to spring at and catch flies brought into its neighbourhood. We shall return to the consideration of these actions a little later on; meanwhile we want to call attention to certain features of the behaviour of a frog devoid of its cerebral hemispheres, features which may be seen in all cases even when all spontaneous movements are wholly absent, and which may be witnessed almost immediately after the operation of removal.

§ 638. We have seen that a frog from which the whole brain has been removed and the spinal cord alone left appears similarly devoid of a 'will'; but the phenomena presented by a frog possessing the middle portions of the brain differ widely from those presented by a frog possessing a spinal cord only. We may perhaps broadly describe the behaviour of a frog from which the cerebral hemispheres only have been removed, by saying that such an animal, though exhibiting no spontaneous movements, can by the application of appropriate stimuli be induced to perform all or nearly all the movements which an entire frog is capable of executing. It can be made to swim, to leap, and to crawl. Left to itself, it assumes what may be called the natural posture of a frog, with the fore limbs erect, and the hind limbs flexed, so that the line of the body makes an angle with the surface on which it is resting. When placed on its back, it immediately regains this natural posture. When placed on a board, it does not fall from the board when the latter is tilted up so as to displace the animal's centre of gravity: it crawls up the board until it gains a new position in which its centre of gravity is restored to its proper place. Its movements are exactly those of an entire frog except that they need an external stimulus to call them forth. They differ moreover fundamentally from those of an entire frog in the following important feature; they inevitably follow when the stimulus is applied; they come to an end when the stimulus ceases to act. By continually varying the inclination of a board on which it is placed, the frog may be made to continue crawling almost indefinitely; but directly the board is made to assume such a position that the body of the frog is in equilibrium, the crawling ceases; and if the position be not disturbed the animal will remain impassive and quiet for an almost indefinite time. When thrown into water, the creature begins at once to swim about in the most regular manner, and will continue to swim until it is exhausted, if there be nothing present on which it can come to rest. If a small piece of wood be placed on the water the frog will, when it comes in contact with the wood, crawl upon it, and so come to rest. If disturbed from its natural posture, as by being placed on its back, it immediately struggles to regain that posture; only by the application of continued force can it be kept lying on its back. Such a frog, if its flanks be gently stroked, will croak; and the croaks follow so regularly and surely upon the strokes that the animal may almost be played upon like a musical, or at least an acoustic instrument. Moreover, provided that the optic nerves and their arrangements have not been injured by the operation, the movements of the animal appear to be influenced by light; if it be urged to move in any particular direction, it seems in its progress to avoid obstacles, at least such as cast a strong shadow; it turns its course to the right or left or sometimes leaps over the obstacle. In fact, even to a careful observer the differences between such a frog and an entire frog which was simply very stupid or very inert, would appear slight and unimportant except in this, that the animal without its cerebral hemispheres is obedient to every stimulus, and that each stimulus evokes an appropriate movement, whereas with the entire animal it is impossible to predict whether any result at all, and if so what result, will follow the application of this or that stimulus. Both may be regarded as machines; but the one is a machine and nothing more, the other is a machine governed and checked by a dominant volition.

Now such movements as crawling, leaping, swimming, and indeed, as we have already urged, to a greater or less extent, all bodily movements, are carried out by means of coordinate nervous motor impulses, influenced, arranged, and governed by coincident sensory or afferent impulses. Muscular movements are determined by afferent influences proceeding from the muscles and constituting the foundation of the muscular sense; they are also directed by means of afferent impulses passing centripetally along the sensory nerves of the skin, the eye, the ear, and other organs. Independently of the particular afferent impulses, which acting as a stimulus call forth the movement, very many other afferent impulses are concerned in the generation and coordination of the resultant motor impulses. Every bodily movement such as those of which we are speaking is the work of a more or less complicated nervous mechanism, in which there are not only central and efferent, but also afferent factors. And, putting aside the question of consciousness, with which we have here no occasion to deal, it is evident that in the frog deprived of its cerebral hemispheres all these factors are present, the afferent no less than the central and the efferent. The machinery for all the necessary and usual bodily movements is present in all its completeness. We may regard the share therefore which the cerebral hemispheres take in executing the movements of which the entire animal is capable, as that of putting this machinery into action or of limiting its previous activity. The relation which the higher nervous changes concerned in volition bear to this machinery may be compared to that of a stimulus, always bearing in mind that the effect of a stimulus on a nervous centre may be either to start activity, or to increase, or to curb, or to stop activity already present. We might almost speak of the will as an intrinsic stimulus. Its operations are limited by the machinery at its command. We may infer that in the frog, the action of the cerebral hemispheres in giving shape to a bodily movement is that of throwing into activity particular parts of the nervous machinery situated in the lower parts of the brain and in the spinal cord; precisely the same movement may be initiated in the absence of the cerebral hemispheres by applying such stimuli as shall throw precisely the same parts of that machinery into the same activity.

Very marked is the contrast between the behaviour of such a frog which, though deprived of its cerebral hemispheres, still retains the other parts of the brain, and that of a frog which possesses a spinal cord only. The latter when placed on its back makes no attempt to regain its normal posture; in fact, it may be said to have completely lost its normal posture, for even when placed on its belly it does not stand with its fore feet erect, as does the other animal, but lies flat on the ground. When thrown into water, instead of swimming, it sinks like a lump of lead. When pinched, or otherwise stimulated, it does not crawl or leap forwards; it simply throws out its limbs in various ways. When its flanks are stroked it does not croak; and when a board on which it is placed is inclined sufficiently to displace its centre of gravity it makes no effort to regain its balance, but falls off the board like a lifeless mass. Though, as we have seen, the various parts of the spinal cord of the frog contain a large amount of coordinating machinery, so that the brainless frog may, by appropriate stimuli, be made to execute various purposeful coordinate movements, yet these are very limited compared with those which can be similarly carried out by a frog possessing the middle and lower parts of the brain in addition to the spinal cord. It is evident that a great deal of the more complex machinery of this kind, especially all that which has to deal with the body as a whole, and all that which is concerned with equilibrium and is specially governed by the higher senses, is seated not in the spinal cord but in the brain. We do not wish now to discuss the details of this machinery; all we desire to insist upon at present is that, in the frog the nervous machinery required for the execution, as distinguished from the origination, of bodily movements even of the most complicated kind, is present after complete removal of the cerebral hemispheres, though these movements are such as to require the cooperation of highly differentiated afferent impulses.

We have thus dwelt at some length on the phenomena presented by the frog for the reason that in this animal the facts which we have described may be demonstrated experimentally with great ease; but, quite apart from what was said above concerning the ultimate development of apparently spontaneous movements, we must not apply at once to all animals, and so to the nervous system generally, the conclusions which we may draw from the behaviour of the frog. As we have already said, the various kinds of animals differ more in the working of their nervous system than in anything else. And in regard to the effect of the removal of the cerebral hemispheres the fish differs markedly from the frog. In the case of most fishes, at all events, the loss of the cerebral hemispheres does not lead to the absence, even the temporary absence, of apparently spontaneous movements. In other words, in the development of the natural movements of the fish the cerebral hemispheres play a far less important part than they do in the case of the frog.

§ 639. Turning now to warm-blooded animals we may remark that in them the removal of the cerebral hemispheres is attended with much greater difficulties than in the case of the frog. Nevertheless, in the bird the operation may be carried out with approximate success. Pigeons for instance have been kept alive for five or six weeks after complete removal of the cerebral hemispheres, with the exception of portions of the crura and corpora striata immediately surrounding the optic thalami; these parts were left in order to ensure the intact condition of the latter bodies.

When the immediate effects of the operation have passed off, and for some time afterwards, the appearance and behaviour of the bird are strikingly similar to those of a bird exceedingly sleepy and stupid. It is able to maintain what appears to be a completely normal posture, and can balance itself on one leg, after the fashion of a bird which has in a natural way gone to sleep. Left alone in perfect quiet, it will remain impassive and motionless for a long time. When stirred it moves, shifts its position; and then, on being left alone, returns to a natural, easy posture. Placed on its side or its back it will regain its feet; thrown into the air it flies with considerable precision for some distance before it returns to rest. It frequently tucks its head under its wings, and at times may be seen to clean its feathers; when its beak is plunged into corn it eats. It may be induced to move not only by ordinary stimuli applied to the skin, but also by sudden loud sounds or by flashes of light; in its flight it will, though imperfectly, avoid obstacles, and its various movements appear to be to a certain extent guided not only by touch but also by visual impressions.

In a certain number of cases this sleepy, drowsy condition passes off and is succeeded by a phase in which the bird, apparently spontaneously, without the intervention of any obvious stimulus, moves rapidly about. It does not fly, that is to say, it does not raise itself from the ground in flight, but walks about incessantly for a long while at a time, periods of activity alternating with periods of repose. It seems, from time to time, to wake up and move about, and then to go to sleep again; and it has been observed that during the night it appears to be always asleep. It is obvious, therefore, that the sleepy, quiescent condition is not due simply to the absence of the cerebral hemispheres, but is a temporary effect of the operation, and that spontaneous movements, that is to say, movements not started by any obvious stimulus, may occur after removal of the cerebral hemispheres. But the movements so witnessed differ from those of an intact bird. They are, it is true, varied; and the variations are in part dependent on external circumstances, the bird being guided by tactile, and, as we have said, visual sensations, or, to be more exact, by impressions made upon the sensory nerves of the skin and on the retina; but they do not shew the wide variations of voluntary movements. The bird never flies up from the ground, never spontaneously picks up corn, and its aimless, monotonous, restless walks, resembling the continued swimming of the frog thrown into the water after being deprived of its cerebral hemispheres, suggest that the activity is the outcome of some intrinsic impulse generated in the nervous machinery in some way or other, but not by the working of a conscious intelligence as in the impulse which we call the will.

Still we must not shut our eyes to the fact that spontaneous movements, whatever their exact nature, are manifested by a bird in the absence of the cerebral hemispheres, and become the more striking the more complete the recovery from the passing effects of the mere operation. Could such birds be kept alive for any considerable time, possibly further developments might be witnessed, and indeed cases are on record where birds have been kept alive for months after the operation, and have shewn spontaneous movements of a still more varied character than those just described; but in such cases the removal of the hemispheres has not been complete, portions of the ventral regions being left behind; and, though a mere remnant left around the optic thalami can hardly be regarded as a sufficient cause for the spontaneity of which we are speaking, a larger mass, still more or less retaining its normal structure, might have a marked effect. And we may here perhaps remark that all these facts seem to point to the conclusion that what may be called mechanical spontaneity, sometimes spoken of as 'automatism,' differs from the spontaneity of the 'will' in degree rather than in kind. Looking at the matter from a purely physiological point of view (the only one which has a right to be employed in these pages), the real difference between an automatic act and a voluntary act is that the chain of physiological events between the act and its physiological cause is in the one case short and simple, in the other long and complex.

These, however, are not the considerations on which we wish here to dwell; we have quoted the behaviour of the bird deprived of its cerebral hemispheres mainly to shew that in this warm-blooded animal, as in the more lowly cold-blooded frog, the parts of the brain below or behind the cerebral hemispheres constitute a nervous machinery by which all the ordinary bodily movements may be carried out. The bird, like the frog, suffers no paralysis when the cerebral hemispheres are removed; on the contrary, though its movements have not been studied so closely as those of the frog, the bird without its cerebral hemispheres seems capable of executing at all events all the ordinary bodily movements of a bird; the most that has been observed has been some slight loss of prehensile power in the feet of raptorial species. And in the bird as in the frog, the afferent impulses passing into the central nervous system, whether they give rise to consciousness or no, play an important part not only in originating but in guiding and coordinating the efferent impulses which stir the muscles to contract, the coordination being effected partly in the spinal cord, but largely and indeed chiefly in the parts of the brain lying behind the cerebral hemispheres. It is further worthy of notice that spontaneity of movement of the kind which we have described, is much more prominent in the more highly developed bird than in the more lowly frog. The cerebral hemispheres are not the only part of the central nervous system which has undergone a greater development in the bird; the other parts of the brain have also acquired a far greater complexity than in the frog.

§ **640**. In the mammal the removal of the cerebral hemispheres is still more difficult than in the bird; the animal cannot be kept alive for more than a few hours; but in some mammals it is possible to observe during those few hours phenomena kindred to those witnessed in the bird and in the frog. The rabbit or rat, from which the whole of both hemispheres has been removed with the exception of the parts immediately surrounding the optic thalami, can stand, run and leap. Placed on its side or back it at once regains its feet. Left alone it generally remains as motionless and impassive as a statue, save now and then when a passing impulse seems to stir it to a sudden but brief movement; but sometimes it seems subject to a more continued impulse to move, in which case death usually follows very speedily. Such a rabbit will remain for minutes together utterly heedless of a carrot or cabbage-leaf placed just before its nose, though if a morsel be placed within its mouth it at once begins to eat. When stirred it will with ease and steadiness run or leap forward; and obstacles in its course are very frequently, with more or less success, avoided. In some cases the animal (rat) has been described as following by movements of the head a bright light held in front of it (provided that the optic nerves and tracts have not been injured during the operation), as starting when a shrill and loud noise is made near it, and as crying when pinched, often with a long and seemingly plaintive scream. So plaintive is the cry which it thus gives forth as to suggest to the observer the existence of passion, this, however, is probably a wrong interpretation of a vocal action; the cry appears plaintive simply because, in consequence of the completeness of the reflex nervous machinery and the absence of the usual restraints, it is prolonged.

Without insisting too much on such results as these, and allowing full weight to the objection which may be urged, that in some of these cases parts of the cerebral hemispheres surrounding the optic thalami were left, there still remains adequate evidence to shew that a mammal such as a rabbit, in the same way as a frog and a bird, may in the complete or all but complete absence of the cerebral hemispheres maintain a natural posture, free from all signs of disturbance of equilibrium, and is able to carry out with success, at all events, all the usual and common bodily movements. And as in the bird and frog, the evidence also shews that these movements not only may be started by, but in their carrying out are guided by and coordinated by afferent impulses along afferent nerves, including those of the special senses. But in the case of the rabbit it is even still clearer than in the case of the bird that the effects of these afferent impulses are different from those which result when the impulses gain access to an intact brain. The movements of the animal seem guided by impressions made on its retina, as well as on other sensory nerves; we may perhaps speak of the animal as the subject of sensations; but there is no satisfactory evidence that it possesses either visual or other perceptions, or that the sensations which it experiences give rise to ideas. Its avoidance of objects depends not so much on the form of these as on their interference with light. No image, whether pleasant or terrible, whether of food or of an enemy, produces an effect on it, other than that of an object reflecting more or less light. And we may infer that it lacks the possession of an intelligent will. But it must always be remembered that some of the phenomena are due to the operation producing other results than the mere absence of the part removed. We must bear in mind that in all the above experiments while the positive phenomena, the things which the animal continues able to do, are of great value, the negative phenomena, the things which the animal can no longer do, are of much less, indeed of doubtful value. The more carefully and successfully the experiments are carried out, the narrower become what we may call the 'deficiency phenomena,' the phenomena which are alone and directly due to something having been taken away. Were it possible to keep the rabbit alive long enough for the mere effects of the operation to pass completely away, we should not only probably witness, as in the case of the bird, a greater scope of movement and more frequent spontaneity, but possibly find a difficulty in describing the exact condition of the animal.

§ **641**. Hitherto attempts to witness similar phenomena in more highly organised mammals such as the dog have failed; these animals do not recover from the operation of removing the whole of both their hemispheres sufficiently to enable us to judge whether they, like the frog, the bird and the rabbit, can carry out coordinate bodily movements in the absence of the hemispheres, or whether in them this part of the brain, so largely developed, has usurped functions which in the lower animals belong to other parts. Our knowledge is largely confined to the experience that when in a dog the cerebral convolutions are removed piecemeal at several operations, the animal may be kept alive and in good health for a long time, many months at least, even after these parts of the brain have been reduced to very small dimensions, and that under these circumstances, the animal is not only able to carry out with some limitations his ordinary bodily movements, but also exhibits a spontaneity obviously betokening the possession not merely of a conscious volition but of a certain amount of intelligence. Unless we are willing to believe that a mere fragment so to speak of the hemispheres can take on most extended powers, such an experience seems to shew that in the dog as in the rabbit and in the bird, the development of so-called higher functions is not limited to the cerebral hemispheres, that the middle and lower portions of the brain in the higher animals as compared with the lower do not increase in bulk merely as the instruments of the hemispheres, but like the hemispheres acquire more and more complex functions. We may perhaps go so far as to ask the question whether the volition and intelligence which such a dog exhibits is not as much the product of the parts lying behind the hemispheres as of the stump left in the front.

If we can thus say little about the condition of a dog without the cerebral hemispheres we can say still less about the monkey, which in all matters touching the cerebral nervous system serves as our best, indeed our only guide for drawing inferences concerning man; but in all probability the monkey in this respect bears somewhat the same relation to the dog that the dog bears to the bird.

In short, the more we study the phenomena exhibited by animals possessing a part only of their brain, the closer we are pushed to the conclusion that no sharp line can be drawn between volition and the lack of volition, or between the possession and absence of intelligence. Between the muscle-nerve preparation at the one limit, and our conscious willing selves at the other, there is a continuous gradation without a break; we cannot fix on any linear barrier in the brain or in the general nervous system, and say 'beyond this there is volition and intelligence, but up to this there is none.'

This, however, is not the question with which we are now dealing. What we want to point out is that in the higher animals, including at least some mammals, as in the frog, after the removal of the cerebral hemispheres, even though conscious volition and intelligence appear to be largely, if not entirely, lost, the body is still capable of executing all the ordinary movements which the animal in its natural life is wont to perform, in spite of these movements necessitating the cooperation of various afferent impulses; and that therefore the nervous machinery for the execution of these movements lies in some part of the brain other than the cerebral hemispheres. We have reasons for thinking that it is situated in the structures forming the middle and hind brain; as we shall see, interference with these parts produces at once remarkable disorders of movement.

SEC. 5. THE MACHINERY OF COORDINATED MOVEMENTS.

§ 642. We may now direct our attention for a while to some considerations concerning the nature of this complex nervous machinery for the coordination of bodily movements, and especially concerning the part played by afferent impulses. Most of our knowledge on this point has been gained by a study of animals not deprived of, but still possessing their cerebral hemispheres, or by deductions from the data of our own experience; but it is possible in most cases to eliminate from the total results the phenomena which are due to the working of a conscious intelligence. Some of the most striking facts bearing on this matter have been gained by studying the effects of operative interference with certain parts of the internal ear, known as the semicircular canals. The details of the structure of these parts we shall describe later on when we come to deal with hearing, but we may here say that each internal ear possesses three membranous semicircular canals, disposed in the three planes of space (one horizontal, and one in each of the two vertical planes, fore and aft and side to side), each membranous canal being surrounded by a bony canal of nearly the same shape, and being expanded at one end into what is called an ampulla, on which fibres of the auditory nerve end. Each membranous canal, in common with the cavity of the internal ear of which it is a prolongation, contains a fluid allied to lymph, called endolymph, and the space between each membranous canal and its corresponding bony canal is in reality a lymph space, containing a fluid which is virtually lymph, though it is called by the special name of perilymph. In birds interference with the semicircular canals produces the following remarkable results.

When in a pigeon the horizontal membranous semicircular canal on either side is cut through, or laid open and plugged with some material such as wax or amalgam, the bird is observed to be continually moving its head from side to side. If one of the vertical canals be similarly treated, the movements are up and down; if both be interfered with, they are diagonal. The peculiar movements may not be witnessed when the bird is perfectly quiet, but they make their appearance whenever it is disturbed, or attempts in any way to stir. When all the canals of one side are operated on, the head is kept turned on one side in a characteristic manner. When the injury is confined to one canal only or even to the canals of one side of the head only, the condition after a while passes away; when the canals of both sides have been divided, it becomes much exaggerated, lasts much longer, and in some cases is said to remain permanently. After these injuries to the canals it is found that the peculiar movements of the head are associated with what appears to be a great want of coordination of bodily movements. If the bird be thrown into the air, it flutters and falls down in a helpless and confused manner; it appears to have lost the power of orderly flight. If placed in a balanced position, it may remain for some time quiet, generally with its head in a peculiar posture; but directly it is disturbed, the movements which it attempts to execute are irregular and fall short of their purpose. It has great difficulty in picking up food and in drinking; and in general its behaviour very much resembles that of a person who is exceedingly dizzy.

It can hear perfectly well, and therefore the symptoms cannot be regarded as the result of any abnormal auditory sensations, such as 'a roaring' in the ears. Besides, any such stimulation of the auditory nerve as the result of the section would speedily die away, whereas these phenomena may last for at least a very considerable time.

The movements are not occasioned by any partial paralysis, by any want of power in particular muscles or group of muscles; though removal of the canals of one side has been described as ultimately leading to diminished muscular force on the same side of the body, the mere diminution of force is insufficient to explain the phenomena. Nor on the other hand are the movements due to any uncontrollable impulse; a very gentle pressure of the hand suffices to stop the movements of the head, and the hand in doing so experiences no strain. The assistance of a very slight support enables movements, otherwise impossible or most difficult, to be easily executed. Thus, though when left alone the bird has great difficulty in drinking or picking up corn, it will continue to drink or eat with ease if its beak be plunged into water or into a heap of barley; the slight support of the water or of the grain seems sufficient to steady its movements. In the same way it can, even without assistance, clean its feathers and scratch its head, its beak and foot being in these operations guided by contact with its own body.

The amount of disorder thus induced differs in different birds; and some movements are more affected than others. As a general rule it may be said that the more complex and intricate a movement, the fuller and more delicate the coordination needed to carry it out successfully, the more markedly is it disordered by the operation; thus after injury to the canals, while a pigeon cannot fly, a goose is still able to swim.

The phenomena are best shewn by and have been chiefly studied in the bird, but they may be witnessed in varying degree in all kinds of vertebrate animals from mammals down to fishes; in the latter class, some of the results have been negative, but careful observation has brought to light the characteristic phenomena in a very clear and decided manner. In all animals, interference with the canals brings about movements of the head or of some part of the body, such as the fins in fishes, and is followed by more or less loss of coordination; in mammals, and indeed in other animals peculiar, often oscillating movements of the eyeballs, differing in direction and character according to the canal or canals operated upon, become especially prominent; as we shall see later on there seems to be some special connection between the ear and the nervous mechanism governing the movements of the eyeball.

Injury to the bony canals alone is insufficient to produce the symptoms; the membranous canals themselves must be divided or injured. The characteristic movements of the head may however be brought about in a bird without opening the bony canal, by suddenly heating or cooling a canal, especially its ampullar terminations, or by the making or breaking of a constant current directed through the canal.

There can be no doubt that these characteristic movements of the head are the result of afferent impulses started in the nervous endings of the auditory nerve over the ampulla of the canal, and conveyed to the brain along that nerve. And that injury to or other stimulation of each of the three canals should produce in each case a different movement of the head, the direction of the movement being different according to the plane in which the canal lies, shews that these impulses are of a peculiar nature. This is further illustrated by the following experiment. If the horizontal canal be carefully laid bare, and the membranous canal opened so as to expose the endolymph, blowing gently over the opened canal with a fine glass cannula will produce a definite movement of the head, which is turned to the one side or to the other, according as the current of air drives the endolymph towards or away from the ampulla. From this it is inferred that a movement of the endolymph over, or an increased pressure of the endolymph on, the nervous endings in the ampulla gives rise to afferent impulses which in some way determine the issue of efferent impulses leading to the movement of the head. It is further suggested that since the planes of the three canals lie in the three axes of space, any change in the position of the head must lead to changes in the pressure of the endolymph on the walls of the ampullae or to movements of endolymph over those walls, and so must give rise to impulses passing up the auditory nerve; and that since every change of position will affect the three canals differently (whereas the changes of pressure of the endolymph involved in a "wave of sound" will affect all three ampullae equally) those impulses will differ according to the direction of the change. A still further extension of this view supposes that since in any one position of the head the pressure of the endolymph will differ in the three ampullae, mere position of the head, as distinguished from change of position, is adequate to generate afferent impulses differing in the different positions.

Let us now for a while turn aside to ourselves and examine the coordination of the movements of our own bodies. When we appeal to our own consciousness we find that our movements are governed and guided by what we may call a sense of equilibrium, by an appreciation of the position of our body and its relations to space. When this sense of equilibrium is disturbed we say we are dizzy, and we then stagger and reel, being no longer able to coordinate the movements of our bodies or to adapt them to the position of things around us. What is the origin of this sense of equilibrium? By what means are we able to appreciate the position of our body? There can be no doubt that this appreciation is in large measure the product of visual and tactile sensations; we recognise the relations of our body to the things around us in great measure by sight and touch; we also learn much by our muscular sense. But there is something besides these. Neither sight nor touch nor muscular sense can help us when, placed perfectly flat and at rest on a horizontal rotating table, with the eyes shut and not a muscle stirring, we attempt to determine whether or no the table and we with it are being moved, or to ascertain how much it and we are turned to the right or to the left. Yet under such circumstances we are conscious of a change in our position, and some observers have been even able to pass a tolerably successful judgment as to the angle through which they have been moved. There can be no doubt that such a judgment is based upon the interpretation by consciousness of afferent impulses which are dependent on the position of the body, but which are not afferent impulses belonging to sensations of touch or sight, or taking part in the muscular sense. We ought not perhaps to forget the possibility of our consciousness being affected by other impulses generated in the tissues by the change of position, such as those due to vaso-motor effects; still it may be urged with great plausibility that the afferent impulses in question are those which we have just referred to as started in the semicircular canals.

If we admit the existence of such ampullar impulses, if we may venture so to call them, and recognise them as contributing largely not only to our direct perception of the position of the head and thus of the body, but also in a more indirect way to what we have called the sense of equilibrium, we should expect to find that when they are abnormal the sense of equilibrium is disturbed, and that in consequence a failure of coordination in our movements results. And the loss of coordination which we described above as resulting from injury to the semicircular canals has accordingly been attributed to a deficiency or disorder of normal ampullar impulses.

It may of course be urged, and indeed has been urged, that the phenomena which follow interference with the canals are due, not to the mere loss of normal impulses, but to the presence of abnormal impulses excited by the injury; and the argument that the mere stimulus of the operation could not produce the more permanent effects often met with, has been met with the contention that the operation has in such cases set up secondary mischief in the cerebellum, with which as we have seen (§ 618) the vestibular nerve is specially connected and which we have some reason for thinking is in some way concerned in the coordination of movements. Careful observation however has shewn that such a contention is invalid; and indeed the whole evidence is in favour of the view that impulses are normally generated in the ampulla according to the movements of the head. Among other arguments in favour of this view may be mentioned the fact that, in fishes, section of the branch of the vestibular nerve going to a particular ampulla produces the same effect as the removal of the ampulla itself.

So far we have spoken of the semicircular canals only, but it is obvious that these are affected by movements of rotation only. If the head (and body) be carried either directly upwards and downwards, or directly forwards and backwards, in the same plane without any rotational movements at all, none of the semicircular canals will be specially affected; yet we are as well aware of such movements as of those of rotation; and afferent impulses generated by such movements must be as necessary to coordination in the same way as those generated by rotational movements. Now the vestibular nerve is distributed not only to the ampullæ of the semicircular canals but also to the parts called the utricle and saccule. And though the experimental evidence is not so decisive as in the case of the semicircular canals, there are strong reasons for thinking that these parts of the vestibule play the same part towards horizontal and vertical movements that the canals do towards movements of rotation. Thus the whole vestibule and the vestibular nerve seems to have a connection with the coordination of movements, and with the appreciation by consciousness of the position of the body in space. We may add that in all probability many of the so-called auditory sacs in invertebrates perform a similar function.

§ **643.** We have dwelt on these phenomena of the semicircular canals because they illustrate in a striking manner the important part played by afferent impulses in the coordination of movements. We saw reason to think (§ 589) that even in an ordinary reflex movement carried out by the spinal cord or by a portion of the cord afferent impulses, other than those which excite the movement, are at work, determining such coordination as is present. In such a case the coordinating afferent impulses are relatively simple in character and start chiefly at all events in the muscles concerned. In an animal possessing the lower parts of the brain, though deprived of the cerebral hemispheres, the coordinating afferent impulses, in accordance with the greater diversity and complexity of the movements which the animal is able to execute, are far more potent and varied. Besides afferent impulses from the muscles, forming the basis of what we have called the muscular sense, afferent impulses from the skin, forming the basis of the sense of touch in the wide meaning of that word, other afferent impulses of obscure character from the viscera and various tissues, and the peculiar afferent ampullar impulses of which we have just spoken, important special afferent impulses borne along the nerves of sight and hearing come into play. The frog, the bird, and even the mammal, deprived of the cerebral hemispheres, though it may shew little signs or none at all of having a distinct volition, is as we have urged indubitably affected by visual and auditory impressions, and whether we admit or no that such an animal can rightly be spoken of as being conscious we cannot resist the conclusion that afferent impulses started in its retina or internal ear produce in its central nervous system changes similar to those which in a conscious animal form the basis of visual and auditory sensations, and we must either call these changes sensations or find for them some new word. Whatever we call them, and whether consciousness is distinctly involved in them or no, they obviously play an important part as factors of the coordination of movements. Indeed, when we appeal to the experience of ourselves in possession of consciousness, we find that though various sensations clearly enter into the coordination of our movements, we carry out movements thus coordinated without being distinctly aware of these coordinating factors. In every movement which we make the coordination of the movement is dependent on the impulses or influences which form the basis of the muscular sense, yet we are not distinctly conscious of these impulses; it is only as we shall see by special analysis that we come to the conclusion that we do possess what we shall call a muscular sense. So again, taking the matter from a somewhat different point of view, many of our movements, markedly as we shall see those of the eyeballs, are coordinated by visual sensations, and when we sing or when we dance to music our movements are coordinated by the help of sensations of sound. In these cases distinct sensations in the ordinary sense of the word intervene; if we cannot see or cannot hear, the movement fails or is imperfect; yet even in these cases we are not directly conscious of the sensations as coordinating factors; it needs careful analysis to prove that the success of the movement is really dependent on the sound or on the sight. These and other facts suggest the view that the point at which the various afferent impulses which form the basis of the sensations of a conscious individual enter into the coordinating mechanism is or may be some way short of the stage at which the complete conversion of the impulse into a perfect sensation takes place. The events which constitute what we may call visual impulses, as these leave the retina to sweep along the optic nerve, are we must admit very different from those which in the appropriate parts of the brain constitute what we may call conscious vision; and probably between the beginning and the end there are progressive changes. It is probable, we say, that these visual events may affect the coordinating mechanism at some stage of their progress before they reach their final and perfect form. If this be so we may further conclude that though, when the whole nervous machinery is present in its entirety, the afferent impulses which take part in coordination must inevitably at the same time give rise to conscious sensations, they might still effect their coordinating work when, owing to the imperfection or lack of the terminal part of the nervous machinery, the impulses failed to receive their final transformation, and conscious sensations were absent. In other words the coordinating influences of sensory or afferent impulses are not essentially dependent on the existence of a distinct consciousness.

§ **644**. We have raised this point partly for the sake of illustrating the working of the coordination machinery in the absence of the cerebral hemispheres, but also in order to aid in the interpretation of the subjective condition which we speak of as giddiness or dizziness or vertigo. We compared the condition of the pigeon after an injury to the semicircular canals to that of a person who is giddy or dizzy, and indeed vertigo is the subjective expression of a disarrangement of the coordination machinery, especially of that concerned in the maintenance of bodily equilibrium. It may be brought about in many ways. When a constant current of adequate strength is sent through the head from ear to ear, we experience a sense of vertigo; our movements then appear to a bystander to fail in coordination, in fact to resemble those of a pigeon whose semicircular canals have been injured; and indeed the effects are probably produced in the same way in the two cases. In what is called Menière's disease attacks of vertigo seem to be associated with disease in the ear, being attributed by many to disorder of the semicircular canals, and cases have been recorded of giddiness as well as deafness resulting from disease of the auditory nerve. Visual sensations are very potent in producing vertigo. Many persons feel giddy when they look at a waterfall; and this is a case in which both the sense of giddiness and the disarrangement of coordination is the result of the action of a pure sensation and nothing else. In the well-known intense vertigo which is caused by rapid rotation of the body visual sensation plays a part when the rotation is carried on with the eyes open, but only a part; for vertigo may be induced, though not so readily, by rotation with the eyes completely shut. In the latter case it has been suggested that the vertigo is caused by abnormal ampullar impulses, but these only contribute to the result, which is in part at least, if not in the main, caused by direct disturbance of the brain. When the rotation is carried out with the eyes open, the vertigo which is felt when the rotation ceases is partly caused by the visual sensations, on account of the behaviour of the eyeballs, ceasing to be in harmony with the rest of the sensations and afferent impulses which help to make up the coordination. The rotation sets up peculiar oscillating movements of the eyeballs (nystagmus), which continue for some time after the rotation has ceased; owing to these movements of the eyeballs the visual sensations excited are such as would be excited if external objects were rapidly moving, whereas all the other sensations and impulses which are affecting the central nervous system are such as are excited by objects at rest. In a normal state of things the visual and the other sensations and impulses, which go to make up the coordinating machinery, are in accord with each other in reference to the events in the external world which are giving rise to them; after rotation they are for a time in disaccord, and the coordinating machinery is in consequence disarranged.

When we interrogate our own consciousness, we find that we are not distinctly conscious of this disaccord; the visual sensations are so prepotent in consciousness, that we really think the external world is rapidly whirling round; all that we are further conscious of is the feeling of giddiness and our inability to make our bodily movements harmonize with our visual sensations. So that even in the cases where the loss of coordination is brought about by distinct sensations what we really appreciate by means of our consciousness is the disarrangement of the coordinating machinery. It is the appreciation of this disorder which constitutes the feeling of vertigo; both the feeling of giddiness and the disordered movements are the outcome, one subjective and the other objective, of the same thing. It is not because we feel giddy that we stagger and reel; our movements are wrong because the machinery is at fault, and it is the faulty action of the machinery which also makes us feel giddy.

We may here perhaps remark that it is an actually disordered condition of the coordinating mechanism which gives rise to the affection of consciousness which we call giddiness, not a mere curtailing of the mechanism or any failure on its part to make itself effective. Complete blindness limits the range of activity of the machinery but leaves the remainder intact, and no giddiness is felt. So again in certain diseases of the nervous system the muscular sense is interfered with over considerable regions of the body, and in these regions coordination fails or is imperfect, but the central machinery is not thereby affected, though its area of usefulness is limited, and no giddiness is experienced; and so in other instances.

Before leaving the subject we may point out that the study of it opens up many interesting views as to the relations of the various afferent impulses determining and influencing the actions of the nervous system. We have already pointed out that the ampullar impulses affect the movements of the eyeballs. Not only when the eyes are opened, but also when they are shut rotation produces nystagmus; in such a case this seems to be due to the ampullar impulses. On the other hand, afferent impulses other than ampullar, more especially visual impulses, may so far replace these as to compensate to a large extent for their absence. Thus the characteristic movements of the head and the incoordination which follow interference with the canals gradually diminish, as a rule, after a while: the absence of the ampullar impulses is compensated for. Now if in an animal, for instance in a pigeon, the cerebral hemispheres are removed before the operation on the canals is performed, not only do the characteristic effects follow that operation, and that perhaps in even more striking manner than in an entire animal, but they remain unchanged until the death of the animal; they are never compensated for. We may infer that the compensation which is effected in the entire animal is effected by means of the cerebral hemispheres. Again, if in a dog after the loss of coordination caused by the removal of the vestibule on both sides has passed off, compensation having been effected, that portion of the cortex which we shall presently speak of as the motor area be removed, incoordination returns, but is after a while again recovered from. In this later stage, however, the animal loses the power of coordination if he be temporarily deprived of visual impulses; in a dark room he cannot walk, or does so with extreme difficulty; compensation is in this case largely effected by means of visual impulses. Lastly, the history of deaf-mutes confirms much which has been advanced above. The causes of deaf-mutism are probably various, but we may suppose that at least in some, if not many of them, the vestibule of the ear is affected. Now careful investigation shews that a large number of deaf-mutes are deficient in the appreciation of the position of their bodies, and even in the coordination of movements. The absence of vestibular impulses is as regards coordination largely compensated for, still the lack may often be detected; many deaf-mutes are unsteady in darkness, and even in the light cannot balance themselves well.

And it is interesting to observe that in the case of a large number of them rotation with the eyes shut does not produce nystagmus.

§ **645**. *Forced Movements.* So far we have dwelt on disorders of the coordinating machinery brought about by the action of various afferent impulses. We have now to call attention to some peculiar phenomena which result from operative interference with parts of the brain, and which in some instances at least may be taken to illustrate how this complex machinery works when some of its inner wheels are broken.

All investigators who have performed experiments on the brain have observed, as the result of injury to various parts of it, remarkable movements which have the appearance of being irresistible, compulsory, forced. They vary much in the extent to which they are developed; some are so slight as hardly to deserve the name, while others are strikingly intense. One of the most common forms is that in which the animal rolls incessantly round the longitudinal axis of its own body. This is especially common after section of one of the crura cerebri, or of the middle and inferior peduncles of the cerebellum, or after unilateral section of the pons, but has also been witnessed after injury to the bulb and corpora quadrigemina. Sometimes the animal rotates towards and sometimes away from the side operated on. Another form is that in which the animal executes 'circus movements,' *i.e.* continually moves round and round in a circle of longer or shorter radius, sometimes towards and sometimes away from the injured side. This may be seen after several of the above-mentioned operations, and in one form or another is not uncommon after various unilateral injuries to the brain. There is a variety of the circus movement, "the clockhand movement," said to occur frequently after lesions of the posterior corpora quadrigemina, in which the animal moves in a circle, with the longitudinal axis of its body as a radius, and the end of its tail for a centre. And this form again may easily pass into a simple rolling movement. In yet another form the animal rotates over the transverse axis of its body, tumbles head over heels in a series of somersaults; or it may run incessantly in a straight line backwards or forwards until it is stopped by some obstacle. These latter forms of forced movements are sometimes seen after injury to the corpus striatum even when a very limited portion of the grey matter is affected. And many of these forced movements may result from injuries which appear to be confined to the cerebral cortex.

When the phenomena are well developed, every effort of the animal brings on a movement of this forced character. Left to itself and at rest the animal may present nothing abnormal, its posture and attitude may be quite natural; but when it is excited to move or when it attempts of itself to move, it executes not a natural movement but a forced one, turning round or rolling over as the case may be. In severe cases the movement is continued until the animal is exhausted; when the exhaustion passes off the animal may remain for some little time quiet, but some stimulus, intrinsic or extrinsic, soon inaugurates a fresh outbreak, to be again followed by exhaustion.

In some of the milder forms, that for instance of the circus movement with a long radius, the curved character of the progression appears simply due to the fact that in the effort of locomotion volitional impulses do not gain such ready access to one side of the body as to the other, the injury having caused some obstacle or other. Hence the contractions of the muscles of one side (the left for instance) of the body are more powerful than the other, and in consequence the body is continually thrust towards the other (the right) side. As is well known we ourselves, when our walk is not guided by visual sensations, tend to describe a circle of somewhat wide radius, the deviation being due to a want of bilateral symmetry in our limbs; and the above circus movement is only an exaggeration of this.

But the other more intense forms of forced movements are more complicated in their nature. No mere blocking of volitional impulses will explain why an animal whenever it attempts to move rolls rapidly over, or rushes irresistibly forwards or backwards. It is not possible with our present knowledge to explain how each particular kind of movement is brought about; and indeed the several kinds are probably brought about in different ways, for they differ so greatly from each other that we only class them together because it is difficult to know where to draw the line between them. But we may regard the more intense forms as illustrating the complex nature of what we have called the coordinating machinery, the capabilities of which are, so to speak, disclosed by its being damaged. Such gross injuries as are involved in dividing cerebral structures or in injecting corrosive substances into this or that part of the brain, must of necessity, partly by blocking the way to the impulses which in a normal state of things are continually passing from one part of the brain to another, partly by generating new unusual impulses, seriously affect the due working of the general coordinating machinery. The fact that an animal can, at any moment, by an effort of its own will, rotate on its axis or run straight forwards, shews that the nervous mechanism for the execution of those movements is ready at hand in the brain, waiting only to be discharged; and it is easy to conceive how such a discharge might be affected either by the substitution for the will of some potent intrinsic afferent impulse or by some misdirection of volitional impulses. Persons who have experienced similar forced movements as the result of disease report that they are frequently accompanied, and seem to be caused, by disturbed visual or other sensations; thus they attribute their suddenly falling forward to the occurrence of the sensation that the ground in front of them is suddenly sinking away beneath their feet. Without trusting too closely to the interpretations the subjects of these disorders give of their own feelings, and remembering what was said above concerning vertigo, we may at least conclude that the unusual movements are in many cases due to a disorder of the coordinating mechanism, brought about by strange or disordered sensory impulses. And this view is supported by the fact that many of these forced movements are accompanied by a peculiar and wholly abnormal position of the eyes, which alone might perhaps explain many of the phenomena.

Somewhat allied to these 'forced movements' is a peculiar rigidity of certain of the skeletal muscles, which is seen in some animals after removal of the cerebral hemispheres (including the corpora striata), together with the optic thalami, and which has been called 'decerebrate rigidity.' The limbs become fixed, with the joints in extreme extension, the neck and the tail are stiffly arched upwards, and all the parts may remain in this condition without intermission for several days. No convulsions or struggling necessarily occur and the breathing is regular and tranquil. The steady, continued tonic contraction of the extensor muscles which causes the rigidity may be temporarily suspended by exciting in a reflex manner the appropriate flexor muscles; the excitation of the flexor entails an inhibition of the antagonistic extensor (cf. 598); but the rigidity returns when the excitation is ended. Since this rigidity of limb is at once and permanently done away by section of the sensory roots of the part, we may conclude that the phenomenon is of a reflex nature; it is however developed by some action of the lower part of the brain determined by the absence of the cerebral hemispheres.

§ 646. The phenomena presented by animals deprived of their cerebral hemispheres shew that this machinery of coordination is supplied by cerebral structures lying between the cerebral hemisphere above and the top of the spinal cord below. But when we ask the further question, how is this machinery related to the various elements which go to make up this part of the brain? the only answers which we receive are of the most imperfect kind.

In the case of the frog we can, after removal of the cerebral hemisphere, make an experimental distinction in the parts left between the optic thalami with the optic nerves and tracts, the optic lobes, and the bulb with the rudimentary cerebellum. When the optic thalami are removed, as might be expected, the evidence of visual impressions modifying the movements of the animal disappears; and it is stated that apparently spontaneous movements are much more rare than when the thalami are intact. When the optic lobes as well as the cerebral hemispheres are removed, the power of balancing is lost; when such a frog is thrown off its balance by inclining the plane on which it is placed, it slips back or falls down; the special coordinating mechanism for balancing must therefore in this animal have a special connection with the optic lobes. But after removal of these organs the animal is still capable of a great variety of coordinate movements: unlike a frog retaining its spinal cord only, it can swim and leap, it maintains a normal posture, and when placed on its back immediately regains the normal posture. The cerebellum of the frog is so small, and in removing it injury is so likely to be done to the underlying parts, that it becomes difficult to say how much of the coordination apparent in a frog possessing cerebellum and bulb is to be attributed to the former or to the latter; probably, however, the part played by the former is small.

In the case neither of the bird nor of the mammal have we any exact information as to the behaviour of the animal after removal of the parts behind the hemispheres, in addition to the hemispheres themselves. Our knowledge is confined to the results of the ablation, or of the stimulation of parts, the cerebellum for instance, in animals in which the rest of the brain has been left intact. Observations of this kind have disclosed many interesting facts, besides the forced movements just referred to, but they have not led to, and indeed could hardly be expected to lead to, any clear views as to the point which we are now discussing. It does not follow that every part, injury or stimulation of which interferes with coordinated movements, or gives rise to definite, forced, or other movements, is to be considered as part of the machinery under consideration. The corpora striata and cerebral hemispheres form, as we have seen, no part of the machinery, yet injury to them may disorder the machinery; and the fact that removal of, or injury to the cerebellum, disorders the machinery is no proof by itself that the cerebellum is an essential part of the machinery.

If we may trust to deductions from structural arrangements, we might be inclined to infer that the anatomical relations of what we have called the tegmental region from the bulb upwards point to its serving as the foundation of the machinery in question. Behind, it has full connections with various parts of the cord, while in front by means of the optic thalami and anterior corpora quadrigemina, if not by other ways as well, it is so far associated with the optic nerves that the path seems open for visual impulses to gain access to it. To this foundation, however, we must add the cerebellum, on account of its relations to it, to the cord, and to the bulb through the restiform bodies, including its ties with the vestibular nerve. And if we add the cerebellum we must also probably add the pons. We may exclude the pes of the crus, since this is composed exclusively of fibres bringing the cerebral hemispheres, including the corpora striata, into connection with the pons, bulb and cord, and so with the coordinating machinery itself, as well as with other parts of the nervous system. And observation as far as it goes supports this deduction from anatomical relationships. We will, however, defer what else we have to say on this point until after we have discussed the carrying out of voluntary movements.

SEC. 6. ON SOME HISTOLOGICAL FEATURES OF THE BRAIN.

§ **647**. The white matter of the brain, as we have already said, like that of the spinal cord consists of medullated fibres, of various sizes, imbedded in neuroglia and supported by septa of connective tissue derived from the pia mater. Save that cells, or even groups or rows of cells—for the most part small cells, about many of which it may be debated whether they are nerve cells or neuroglia cells—are frequently seen between the fibres and bundles of fibres, the white matter of the brain seems essentially identical with that of the spinal cord.

The grey matter of the brain in general also resembles the grey matter of the spinal cord in consisting of nerve cells with axons and branching dendrites, imbedded in neuroglia. Fibres from the white matter pass into the grey matter to effect synapses with the cells, and axons of cells of the grey matter pass into the white matter to become nerve fibres; hence the grey matter like that of the cord is also traversed by what are ordinarily spoken of as non-medullated fibres and fibrils, and medullated fibres mostly fine, but to some extent of ordinary size. In the case of most of the nerve cells, the axon becomes a medullated nerve fibre, and generally but not always giving off collaterals, often runs for a considerable distance. In certain cells however, the cells of Golgi, the axon never becomes a medullated nerve fibre and never leaves the grey matter but at no great distance from the perikaryon branches in a rapid and extensive manner; such a distinction, as we have seen, is met with also in the spinal cord. In the grey matter of the brain are found also cells having other very special features; these are not present in the spinal cord and form perhaps the distinguishing feature of the former.

The 'central' grey matter is extremely like that of the cord except that the nervous elements are imbedded in a relatively larger quantity of neuroglia. Immediately underneath the epithelium lining the several ventricles and the aqueduct, the neuroglia is especially developed, forming a distinct layer which may be regarded as a continuation of the central gelatinous substance of the spinal cord, and which with the epithelium overlying it forms what is known as the *ependyma*. The 'nuclei' of the cranial nerves are, as we have seen, comparable to the groups of nerve cells in the spinal cord.

A great deal of the grey matter of the brain may be spoken of as more 'diffuse' or 'scattered,' more broken up by bundles of fibres than is the case in the spinal cord. The 'reticular formation' of the bulb, and of the tegmental region, is an extreme form of this diffuse grey matter. And even in such collections of indubitable grey matter as the corpus striatum, optic thalamus and the like, the pure grey matter, if we may use the term, is much more interrupted and broken up by conspicuous bundles of white fibres than is the case in any region of the spinal cord. In the corpora quadrigemina too the grey matter is broken up by sheets or bundles of white matter.

The nerve cells of the several collections of grey matter are not all alike; they present in different regions differences in size, form, and in other characters. The cells of the nucleus caudatus, for instance, are rather small and often round or spindleshaped, while those of the optic thalamus are large, branched and rich in pigment. The cells of the substantia nigra are spindleshaped, of moderate size, and so loaded with black pigment (in man) as to justify the name; those of the locus cæruleus are very large and spherical, with just so much pigment as to give a bluish tint. Our knowledge, however, of the physiological significance of the finer histological characters of most of these various kinds of cells is too limited to justify our dwelling on them. Two regions of grey matter alone call for special description here, the cortex cerebri and the superficial grey matter of the cerebellum.

The superficial grey matter of the cerebellum.

§ **648**. The surface of the cerebellum is increased by being folded or plaited into leaf-like folds, and each of these primary folds is similarly folded into a number of secondary, also leaf-like, folds or lamellæ. Each of these lamellæ consists of a central core of white matter, the fibres of which pass inwards to, and contribute to form the central white matter of the cerebellum, and of a superficial layer of grey matter. A section through a lamella perpendicular to the surface (Fig. 128) shews that the grey matter consists essentially of two layers: a layer lying next to the white matter formed by densely crowded small cells, called the *nuclear layer*, and between this and the superficial pia mater a much thicker layer of peculiar nature, called the *molecular layer*. Between these two layers lies a row of very large and remarkable cells, called *the cells of Purkinjé*, the bodies of which abut on the nuclear layer, and the long dendrites of which traverse the molecular layer; these cells so placed may be said to constitute a third layer. These are fundamental parts, for the molecular and the nuclear layers may be recognized even in the lower vertebrates, and in all become distinguished at an early stage of development; the cells of Purkinjé also appear in the most simple forms.

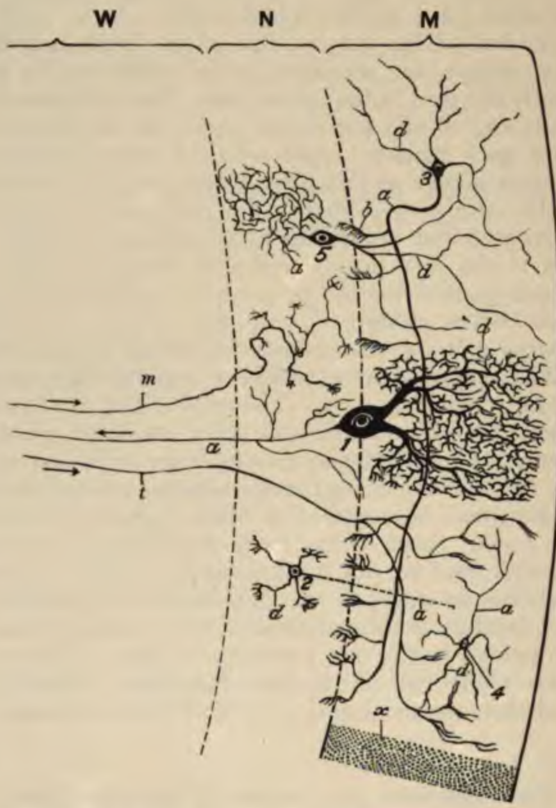

Fig. 128. Diagram of a section of a Leaflet of the Cerebellum taken in the transverse plane.

M. Molecular layer. *N*. Nuclear layer. *W*. White matter.

1. Cell of Purkinjé. 2. Spider-like cell of the nuclear layer. 3. Basket-cell; *b* a basket. For the sake of clearness the basket belonging to the particular Purkinjé cell shewn in the figure has been omitted. 4. Other cells in the molecular layer. 5. Cell of Golgi.

t. tendril fibre; *m*. moss fibre.

a. axon, *d*. dendrite in the case of each cell. The arrows indicate the assumed direction of nervous impulses. In the area x is shewn the punctated appearance of the molecular layer as seen in transverse section.

Before proceeding further, we may here remark that a section of a lamella, that is one of the secondary not one of the primary folds, while still remaining a vertical section (that is perpendicular to the surface) may be carried through the lamella in different planes, and that of these several planes the sections taken in two of them are especially instructive, namely, the one taken in what we may call the longitudinal plane (Fig. 128 A), passing from the top of the lamella to its base, and the one taken at right angles to the former (Fig. 128), in what we may call the transverse plane. The nuclear layer and the molecular layer present the same broad features in both longitudinal and transverse sections, but the long, much branched dendrites of the cells of Purkinjé since they run in the transverse plane are adequately seen in transverse sections only; longitudinal sections shew only their profiles.

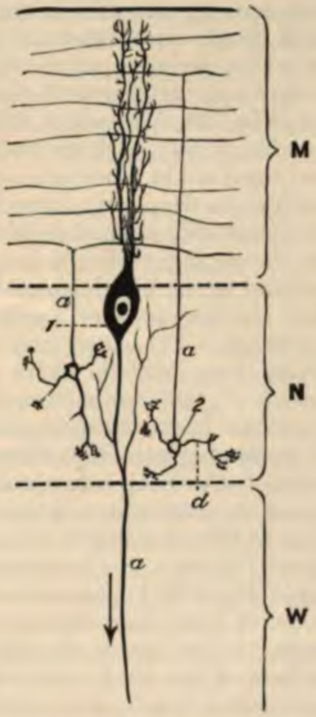

FIG. 128 A. THE SAME TAKEN IN THE LONGITUDINAL PLANE.
Both figures are wholly diagrammatic.

The molecular layer (Fig. 128, *M*) owes its name to the fact that with ordinary modes of preparation, and in sections taken in certain planes it appears chiefly composed of a ground substance which is granular or dotted as if made up of an aggregation of molecules. The dots however are the transverse sections of fine fibrils, some neuroglial in nature, but the great majority nervous. The layer consists of a bed of neuroglia composed as elsewhere of neuroglia fibrils and scattered neuroglia cells, and of nervous elements, namely, of the dendrites of the cells of Purkinjé, of special cells proper to the layer, each with its dendrites and axon, and of a multitude of fibrils proceeding either from the underlying nuclear layer or from the still deeper white matter. The distinguishing feature of the layer is the presence of the multitudinous fibrils whose section gives the 'molecular' appearance.

The nuclear layer (Fig. 128, *N*), as seen in specimens prepared and stained in the ordinary way, appears to consist of a mass of nuclei closely crowded together in a bed of a reticular nature; and since the nuclei usually stain deeply the layer stands out in strong contrast to the much less deeply stained molecular layer. Some of the nuclei are nuclei belonging to the neuroglia which supports the nervous elements, and to the blood vessels which nourish them, but the great majority are the nuclei of nerve cells having special characters and connections. The silver and the methylene-blue methods of preparation have enabled us to recognize that this superficial grey matter of the cerebellum, including both the molecular and the nuclear layer, consists essentially of different kinds of nerve cells possessing special features, and making connections on the one hand with each other, and on the other hand with the underlying white matter in a remarkable and intricate manner. The keystone of this remarkable arrangement seems to be supplied by the cells of Purkinjé, and to these we must first turn.

The cell of Purkinjé (Fig. 128, 1) possesses a large (40 μ by 30 μ) flask-shaped body or perikaryon, surrounding a large conspicuous, clear, rounded nucleus; it has much the appearance of a large ganglion cell. The base of the flask rests on the nuclear layer, and from it there proceeds a single axon which, passing through the nuclear layer somewhat obliquely, and in its passage acquiring a medulla, joins the central white substance as a medullated fibre. The cells form in any one section a single layer only, but since this covers the nuclear layer over the whole of the lamella, a considerable number of the fibres of the white central matter, though only a small fraction of the whole, are thus derived from these cells of Purkinjé. As it is passing through the nuclear layer, and even beyond, the axon gives off fine collaterals which, branching extensively, run back into the nuclear and also into the molecular layer. The narrowed neck of the flask running outward in the molecular layer divides in an arborescent fashion into a large number of dendrites, which, spreading out laterally in the transverse plane and stretching as far as the surface, ramify through the molecular layer, and are eventually lost to view as exceedingly fine fibrils, contributing to the fibrillar or dotted aspect of the molecular layer.

Specially connected with the perikaryonic body of the cells of Purkinjé are certain conspicuous nerve cells in the molecular layer, which may be spoken of as 'basket-cells.' These (Fig. 128, 3), which, lying at different levels, are the most numerous nerve cells of the layer, possess numerous dendrites, ramifying to some distance from the perikaryon. The well-developed axon of each cell, running for some distance in the transverse plane more or less concentric with the surface of the lamella, sends inwards at intervals in succession collaterals, each of which, passing to the perikaryon of a cell of Purkinjé, branches out into a sort of basket-work (Fig. 128 *b*) closely surrounding it; in this peculiar fashion each of these cells forms synapses with a number of the cells of Purkinjé.

No less characteristic are the cells whose nuclei supply the large part of the nuclei of the nuclear layer. In each of these (Fig. 128, 2) the perikaryon is slender, and from it spread out, in spider fashion, a number of relatively short dendrites, each ending in a peculiar arborescence not unlike a muscle end-plate; these dendrites supply a great deal of what in ordinary preparations appears as a reticular bed for the nuclei. The axon runs straight for the molecular layer, apparently without giving off any collaterals, and at a varying level bifurcates at right angles into two branches (Fig. 128 A) which run for a considerable distance in the longitudinal plane, also apparently without giving off collaterals. Since these cells are very numerous, and the axon of each thus provides two fibrils, the molecular layer throughout its depth is traversed by a very great number of longitudinally running fibrils; and it is the sections of these which chiefly give rise to the dotted appearance so characteristic of transverse sections.

These three kinds of cells, those of Purkinjé, the basket-cells of the molecular layer, and the cells of the nuclear layer just described, may perhaps be regarded as the most important cells; but there are others.

In the molecular layer are cells (Fig. 128, 4) smaller than the basket-cells, whose dendrites and axons are both confined to the molecular layer, but whose axons though they branch do not bear any basket-like terminations.

In the nuclear layer or on the border of the nuclear and molecular layers are relatively large cells (Fig. 128, 5) of the kind known by the name of the 'cells of Golgi.' They are characterized by the axon rapidly dividing, soon after it has left the cell, into a number of branches in a dendritic fashion. This branched axon is directed to and ends in the nuclear layer, while the dendrites lie in the molecular layer.

The axon of the Purkinjé cell passes, as we have seen, into the white matter forming the core of the lamella to become one of the constituent fibres of the core. But other fibres of the core are connected with the grey matter in a different way. Of these we can distinguish two kinds. One kind traced from the core through the nuclear layer into the molecular layer, there branches into a number of fibrils which cling after the fashion of a climbing plant round the dendrites of the cell of Purkinjé; this kind of fibre has been called the 'clinging' or 'tendril' fibre (Fig. 128, *t*). The other kind (Fig. 128, *m*) ends in the nuclear layer, by dividing into a number of fibrils, each of which terminates by an arborescence in connection with the cells of the nuclear layer, the whole ending, having in silver preparations a 'mossy' appearance; hence this kind of fibre has been called the 'moss' fibre.

It is obvious from the above description, though this is by no means an exhaustive one, that the arrangements of the nervous elements in the superficial grey matter of the cerebellum afford opportunity for a most complex play of nervous impulses. Continuing to assume that in a nerve cell the usual course of impulses is centripetal along the dendrites towards the perikaryon and centrifugal along the axon, we may picture to ourselves that play somewhat as follows. Impulses from the spinal cord or other parts passing along the 'tendril' fibres affect through synapses the dendrites of Purkinjé cells, and so give rise to new impulses which pass away along the axon of the Purkinjé cell from the cerebellum to other parts. This is the simple, short, direct course. But other impulses if carried by the 'moss' fibres, though passing in the same direction, would spend themselves on the cells of the nuclear layer. The new impulses thus generated would pass into the molecular layer and spread along the bifurcating fibrils for a long distance in opposite directions in the longitudinal plane. Here by the synapses of the longitudinal fibres with the dendrites of the Purkinjé cell, they would affect these cells in a direct manner; at the same time through synapses with the basket-cells they would affect the same Purkinjé cells in an indirect manner, and since the axon of each basket-cell bears baskets for several Purkinjé cells a number of these Purkinjé cells would be 'associated' in the same event.

A further complexity of play is afforded on the one hand by the cells of Golgi, whose dendrites, lying in the molecular layer, pass on and, through the much branching axon, distribute to the nuclear layer the impulses so variously excited in that molecular layer, and on the other hand by the smaller cells of the molecular layer, which taking up impulses by their dendrites in one spot, pass them on to other parts and other structures in the molecular layer.

And it is perhaps worthy of note that all this complex play of impulses takes place in a part of the brain, whose functions, whatever they be, are simplicity itself compared with those of the cerebral cortex, to which we must now turn.

We may here add the remark that the large body of the cell of Purkinjé lies, as indeed do the other nervous elements, in an appropriate space in the bed of neuroglia. Between the surface of the cell and the wall of neuroglia is a space, generally so narrow as to be potential rather than actual, but which may sometimes be considerable. Whether small or large it contains lymph, and the cavity in which the cell lies is in connection with the lymphatics of the brain. Each cell then lies in a lymph space; but we merely mention the fact now; we shall have to return to the matter when we come to deal with the lymphatic and vascular arrangements of the brain and spinal cord.

The Cerebral Cortex.

§ **649**. While the superficial grey matter of the cerebellum does not differ strikingly as to its histological features in different regions, very considerable differences are observed in different regions of the cerebral cortex. A general plan of structure may be recognized, but as we pass from one part of the cerebral surface to another we find modifications continually taking place. We must content ourselves here with attempting a description of the general plan followed by an indication of the more striking characteristics of certain regions.

The dominant feature of the mammalian brain is the development of the cortex of the cerebral hemispheres with the underlying and contingent white matter, the two constituting what is sometimes spoken of as the 'pallium'; and in the ascending series of mammals this pallium becomes more and more dominant, reaching its fullest stage in man. In the fish it is hardly more than an extension of the ependyma surrounding all the ventricles of the brain; but in the amphibia, for instance in the frog, we may recognize the plan of its future structure foreshadowed in a very simple form. In a vertical section of the cerebral hemisphere of the frog (Fig. 129) the space between the pia mater and the ciliated epithelium lining the ventricle is occupied by two layers, one superficial and thin, consisting of many fibres and few cells, the other deeper and thicker, consisting of many cells and few fibres; and a very similar arrangement obtains in the embryonic mammalian brain at a certain stage. The former thin superficial layer, which subsists as a distinct layer in the brains of all the higher animals, has been called the 'molecular layer'; the latter, which in higher animals is differentiated into several layers, may be called at first simply "the layer of cells." The molecular layer consists largely of branching fibres and fibrils, whose sections as in the molecular layer of the cerebellum give rise to a dotted or "molecular" appearance. Among these are scattered a few cells whose branches whether dendrites or axons run for the most part in a longitudinal direction. The cells forming the underlying "layer of cells" are to a large extent cells still in

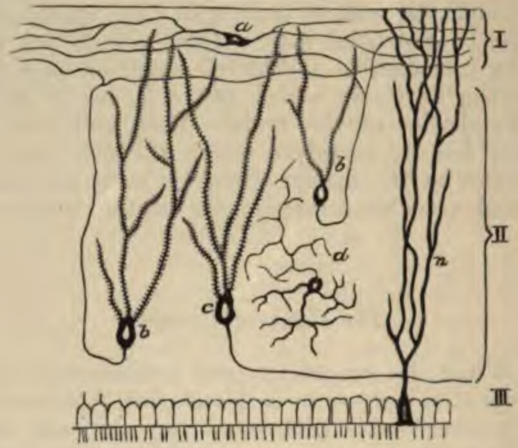

Fig. 129. Diagram of the nerve cells of the Cerebral Hemisphere of the Frog.
I. Molecular layer. II. Pyramid cell layer. III. Ependyma.
a. horizontal cells of the molecular layer. *b*, *b*. pyramidal cells with basal axons curving upward to join the tangential fibres of the molecular layer. *c*. pyramidal cell with axon running down toward the ependyma above which it runs contributing to a rudimentary medullary layer of fibres. *d*. a Golgi cell. *n*. a neuroglia cell.

the simple epithelial stage, out of which as we have seen (§ 563) all the cells of the central nervous system are developed; these have not as yet become differentiated into distinctly nervous cells. Among them however are a number of cells with obvious nervous characters; and these are of more than one kind. Some of them resemble the cells which we shall presently speak of as 'pyramidal' cells, in so far as that their dendrites which run up towards and largely end in the molecular layer, bear short tooth or bristle-like processes giving them, in silver and methylene blue preparations, a very characteristic appearance. In the case of many of these cells, the axon, bearing collaterals, turns back and so running up enters the molecular layer (Fig. 129, *b*). In the case of others, fewer in number, the axon is directed downward and taking up a position just above the epithelium of the ventricle runs backward to other parts of the brain (Fig. 129, *c*); it thus helps to form the rudiment of the future white matter of the hemisphere. Other cells again, like the cells of Golgi elsewhere, possess not a long axon but a short and much branched one which is usually directed upwards towards the molecular layer, the dendrites spreading in the opposite direction (Fig. 129, *d*). Lastly some of the epithelium cells, losing their cilia and becoming so far inert, develope their cell body into branches which spread upwards through both layers to the surface, and so form a supporting scaffold for the other elements (Fig. 129, *n*); these are neuroglia cells.

As we pass upwards through the scale of animals we find that the molecular layer, though increasing in complexity, is not greatly altered. The layer of cells on the contrary becomes largely modified. All the cells composing it become definitely developed into either nerve cells or neuroglia cells, and into many different kinds of nerve cells in such a way that the single layer obtaining in the frog is in the mammal differentiated into several layers. Many of the cells continue to send their axons in an ascending direction to or towards the molecular layer; but an increasing number, taking on as we shall see the definite characters of pyramidal cells, send their axons in a descending direction and thus increase the white matter underlying them; this increase is further assisted by the growth of axons coming from cells in other parts of the brain, and ending in the cortex. Put briefly the development of the cortex, or rather of the pallium, in the animal series (and the embryonic development in the individual affords a close parallel) consists on the one hand in the multiplication and differentiation of the cells in what we have called in the frog the layer of cells, and on the other in the establishment of ties in the form of fibres between these cells and cells in other parts of the central nervous system, either in other divisions of the brain or in the spinal cord or in other areas of the cerebral hemispheres; as we have seen the great pyramidal tract is in man the last such tie to be formed. The superficial molecular layer though making its appearance at the first, and always remaining of great importance, becomes, owing to the greater development of the underlying parts, relatively less in the higher animals.

Turning now to the mammal, we may say that the cortical grey matter, having, in man, an average thickness of about 3 mm., but varying considerably in different regions from 1·8 mm. in some parts of the occipital lobe to 4·2 at the dorsal summit of the precentral convolution, is, like other grey matter, composed of nerve cells, and of nerve fibres and fibrils supported by neuroglia. The nerve cells are scattered, and appear, in sections prepared in the ordinary way, to be imbedded in, and separated from each other by a not inconsiderable but variable quantity of somewhat peculiar ground substance, not unlike that which forms so large a part of the molecular layer of the cerebellum. Part of this ground substance, which apparently is not confined to any particular layer, but stretches throughout the thickness of the cortex, is undoubtedly neuroglial in nature, but part, and the greater part, is nervous in nature; it is largely composed of fine fibrils traversing it in various directions, the transverse sections of these fibrils giving it a characteristic dotted or 'molecular' appearance; and the majority of these fine fibrils are nervous in nature, the remainder being neuroglial fibrils. It is, to a much greater extent than is the molecular layer of the cerebellum, traversed by medullated nerve fibres, especially by fine medullated fibres.

The nerve cells imbedded in this ground substance in more or less distinct layers are of various kinds. The most conspicuous, abundant and characteristic nerve cells found in the cortex of all regions of the cerebrum, are those which from their shape are called *pyramidal cells.* These vary much in size and have been distinguished as 'small pyramidal' cells averaging 12 μ in length by 8 μ in breadth, and 'large pyramidal' cells, sometimes called 'ganglionic cells,' of which the medium size is about 40 μ in length by 20 μ in breadth. Some of the large kind, occurring in special regions, are of very great size, 120 μ by 50 μ, and have been called 'giant cells.'

The features of a 'large pyramidal' cell (Fig. 130) are very characteristic. Such a cell appears in a well-prepared vertical section of the cortex as an elongated isosceles triangle placed vertically, with the base looking towards the underlying white substance and the tapering apex pointing to the surface. The cell substance is finely granulated or fibrillated, the fibrillæ sweeping round in various directions. As in the case of many other nerve cells, parts of it, staining more deeply with ordinary staining reagents than the rest, are disposed in masses of a more or less spindle-shape, the so-called chromatin spindles (Fig. 130, *chr.* &c.); it also not unfrequently contains definite pigment granules. In the midst of this cell substance rather near the base lies a large, clear conspicuous round or oval nucleolated nucleus. At the base the cell substance is prolonged into a number of processes. One of these, generally starting from about the middle of the base, may be recognized as the axon (Fig. 130, *a*); the fibre to which it gives origin sweeps with a more or less curved course into the subjacent white matter. Its further course is varied; it may pass to lower parts of the brain as a "projection" fibre may for instance become a fibre of the pyramidal tract, or it may pass by the corpus callosum to the cortex of the opposite hemisphere as a "commissural" fibre, or it may pass to another area of the cortex of the same side as an "association" fibre. It generally gives off collaterals, and these may have a different destination from the fibre itself, some trending back at once to the same area cortex, or for instance passing to another area of the same cortex or to the opposite cortex, while the fibre itself joins the pyramidal tract or passes at least to other parts of the brain. In some instances, again, the axon bifurcates and so gives rise to two fibres which pass to different destinations. The other processes from the base are dendrites, basal dendrites (Fig. 130, *d*), which, rapidly branching into fine fibrils, are soon lost to view in the ground substance. The apex of the triangle is developed into a dendrite, apical

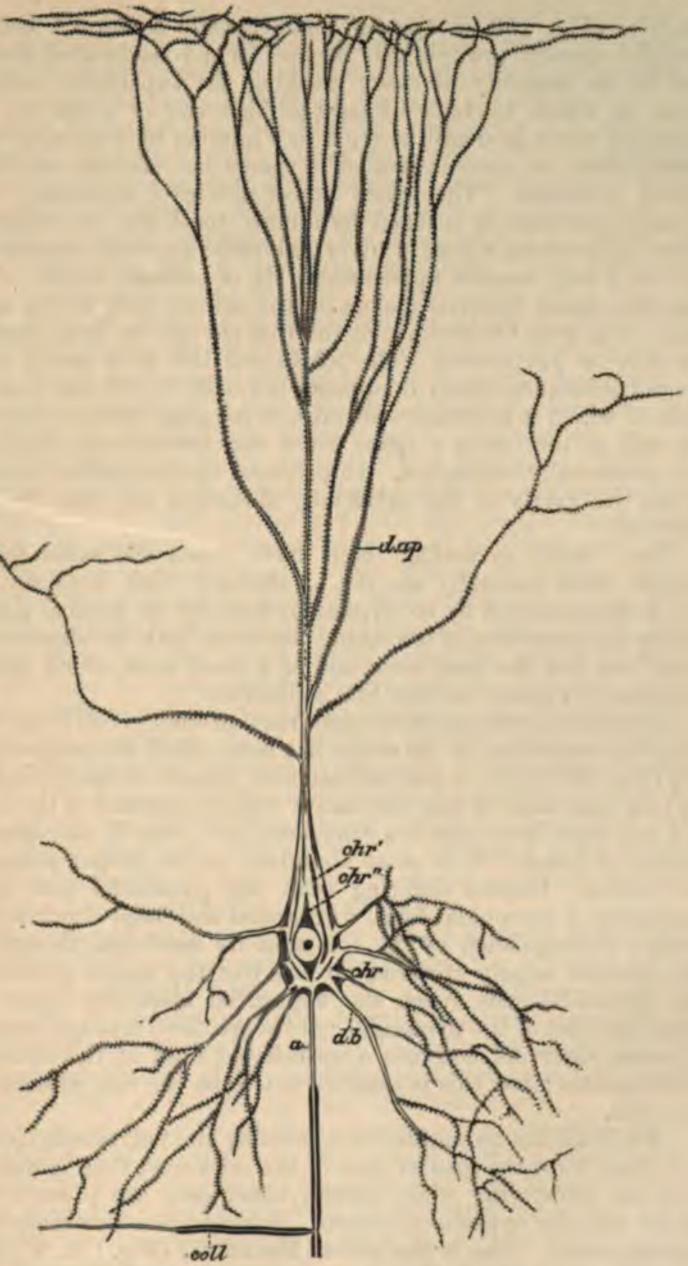

FIG. 130. DIAGRAM OF A PYRAMID CELL.

a. axon with *coll.* collateral. *d. b.* basal dendrites. *d. ap.* apical dendrites. *chr. chr'. chr''.* the three kinds of chromatin spindles in the perikaryon.

dendrite (Fig. 130, *d. ap.*), of characteristic features. Running straight upward towards the surface for a considerable distance, and in the majority of cases reaching the superficial molecular layer, to which we have already alluded and of which we shall presently speak in detail, it ends in a number of branching fibrils, having along its course given off a sparse but variable number of lateral branches. The whole apical dendrite, especially in its terminal portions, is marked by minute tooth-like or bristle-like lateral projections, which, in silver and methylene-blue preparations, give it a very notable appearance. It is perhaps worthy of note that this apical dendrite makes its appearance early in the animal scale; it is seen for instance in the frog though the basal dendrites are here as yet absent. The whole cell lies in a cavity of the ground substance which it appears normally to fill, but from the walls of which it sometimes shrinks, developing between itself and the wall of the cavity a space which may contain not only lymph but occasionally leucocytes. In prepared specimens the retraction within its cavity of the artificially shrunken cell may be often observed.

The 'small pyramidal' cells have much the same features though these naturally are not so distinct; that is to say, each cell is characterised by its pyramidal form, by its vertical position, and by the possession of branching dendrites, both the characteristic apical one and the basal ones, and of a basal axon which, directed downwards, appears to bear fine collaterals.

Another less abundant but still frequent kind of cell is one which from the variability of its shape has been called the *polymorphous* cell (Fig. 131 *P*). It is not unfrequently spindle-shaped, lying with its long axis more or less concentric with the surface of the cortex, and has then been called a 'fusiform' cell; but it may assume a variety of forms. It is most abundant in the deeper portions of the cortex. Besides differing from the pyramidal cell, in not possessing a pyramidal form, with apical and basal dendrites, it is further distinguished by the fact that its dendrites, though they are directed largely upwards, do not, like the apical processes of the pyramidal cells, reach the superficial molecular layer. The axon like that of the pyramidal cell sweeps down into and according to some observers becomes a medullated fibre of the underlying white matter; but this is asserted not to be the case at least in all the cells.

While all the pyramidal (and possibly the polymorphous cells), and these form the greater part of the cells, send their axons down into the underlying white matter, other cells are present whose axons take the opposite direction. Among these two kinds can be distinguished. One is the cell of Martinotti (Fig. 131, *M*), whose dendrites spread out in the usual way from the perikaryon and whose axon, acquiring apparently a medulla, rises up towards the surface, giving off collaterals and ends, in most cases at least, by branching in the superficial molecular layer. The other cell is the cell of Golgi (Fig. 131, *G*), the axon of which, though trending upwards, here as elsewhere rapidly divides into a large number of relatively short branches, apparently without acquiring a medulla.

Lastly, there occur, especially in the superficial molecular layer of animals at least, if not of man, cells (Fig. 131 *c*), sometimes stellate or 'polygonal' but more frequently 'fusiform' and disposed horizontally, bearing a number of processes so much alike, that it has been debated whether any of them, and if so which, are axons, or whether all of them are dendrites. These have been called 'pluripolar' cells.

In addition to these several kinds of nerve cells, there are scattered through the cortex, and especially abundant in the superficial layer, branched cells which are neuroglial in nature.

The medullated nerve fibres which take part in the cortex may be considered provisionally as forming two categories. In the first place fibres sweep up vertically into the cortex from the subjacent 'central white matter,' taking at first a curved course as they enter into the grey matter and then appearing to run straight towards the surface. These are arranged in the deeper levels in bundles, the 'medullary rays' (Fig. 131, *m. r.*), leaving vertical columns of the grey matter between them; but at more superficial levels the bundles spread out and are gradually lost to view. Some of these fibres are the axons of the pyramidal and polymorphic cells, and may be presumed to be engaged in carrying impulses from the cortex through the white matter to one or other of the destinations mentioned above. Others, however, are axons or collaterals of axons which have come from cells situate either in other parts of the brain, in the optic thalami for instance, or in the cortex of the opposite hemisphere, or in some other area of the cortex of the same side. These may be presumed to be engaged in carrying impulses to the cortex. They end in various depths of the cortex but largely in the superficial layer.

In the second place, besides these vertical fibres of the ordinary medullated kind, an exceedingly large number of fibres of the peculiar fine medullated kind, many of them being probably collaterals, run in various directions, forming a dense network in the ground substance of the grey matter between the cells. We may add that this system of fine medullated fibres is of late growth and is not fully developed in man until adult life.

Many of the medullated fibres, coarse as well as fine, take a horizontal direction parallel to the surface, and in certain regions are specially developed into a layer or into two layers so as to form a horizontal streak or streaks, one being sometimes called 'Gennari's' and the other 'Baillarger's' band (Fig. 131, *y* and *z*).

The vascular pia mater invests closely as we have said the whole surface of the cortex, dipping down into the sulci; and from it, as in the case of the spinal cord, processes carrying blood vessels

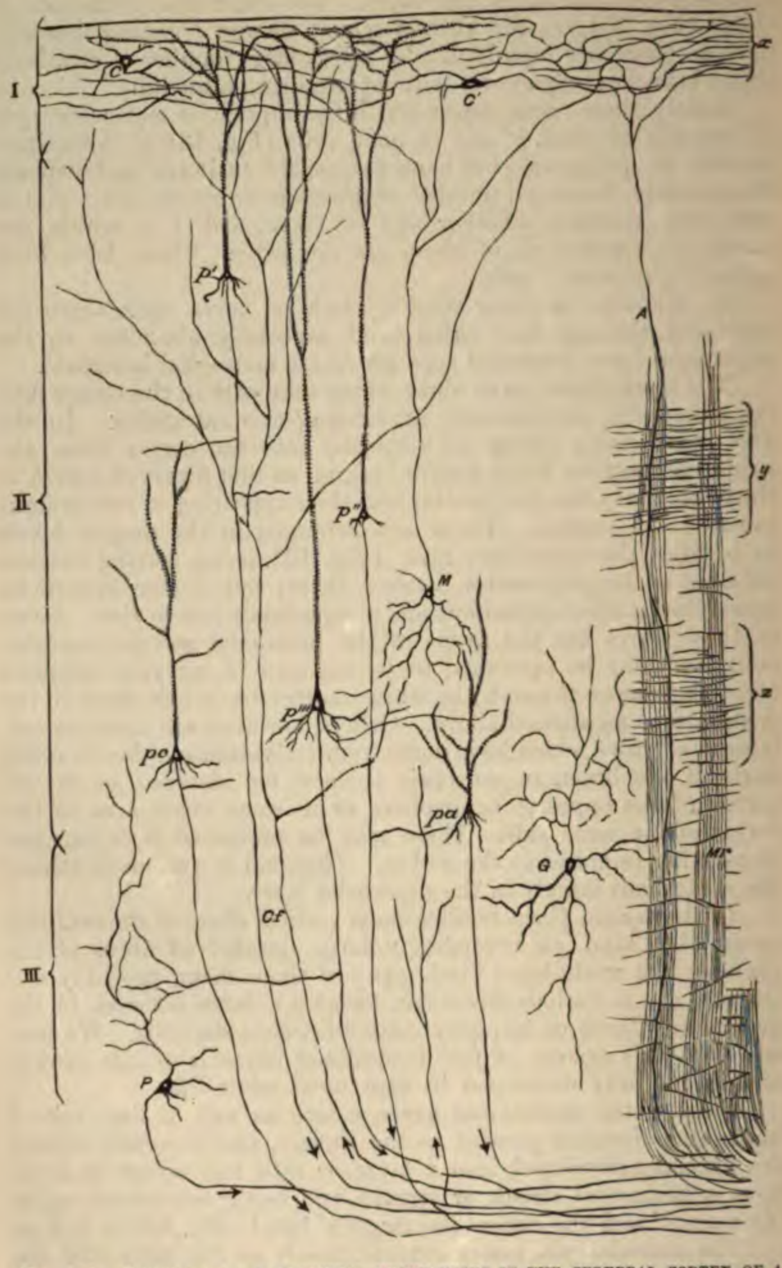

FIG. 131. SCHEME OF THE PRINCIPAL NERVE CELLS IN THE CEREBRAL CORTEX OF A MAMMAL.

I. Molecular layer. II. Layer of pyramid cells. III. Layer of polymorphous cells.

$p'p''p'''$ pyramid cells. *pa.* a pyramid cell whose axon reaches an adjoining region of cortex as an association fibre. *p.c.* a pyramid cell whose axon passes to the opposite hemisphere (via corpus callosum or anterior commissure) as a commissural fibre. *M.* a cell, 'Martinotti cell,' whose axon runs outwards toward the surface of the cortex. *G.* a cell, 'Golgi cell,' with a short much branched axon—the axon is not always turned upwards as in the instance figured. *c.* a "polygonal" cell of the molecular layer. *c'* a "fusiform" cell of the molecular layer. *A.* an "association" or "commissural" nerve fibre, the axon of a distant cell. *Cf.* a nerve fibre, the axon of a cell belonging to the fillet or the optic thalamus. *P.* a cell of the polymorphous layer.

m.r. medullary ray of medullated fibres. *x.* outermost layer of tangential fibres. *y.* middle layer of tangential fibres (Gennari's band). *z.* inner layer of tangential fibres. (Baillarger's band.)

and bearing lymph spaces pass inwards to supply the grey matter with blood. But while, as we shall see later on, the supply of blood vessels to the grey matter is considerable, the truly connective tissue elements of the pia mater processes are soon merged into neuroglia. Immediately beneath the pia mater forming the immediate surface of the cortex is a thin layer consisting of neuroglia only.

§ **650**. The nerve cells of the above several kinds are arranged more or less distinctly in layers parallel to the surface, so that the whole thickness of the cortex may by means of them be, more or less successfully, divided into a series of zones, one above the other; and we may, as we have said, recognize on the one hand a general arrangement common to the whole surface, and on the other hand modifications existing in the several regions. The most satisfactory division is probably that into three zones or layers, though four, five or even more have been described. These layers are usually counted from the surface inwards.

The third layer (Fig. 131, III.), lying next to the central white matter, fairly uniform in characters and thickness (about 1 mm.) over the greater part of the brain is characterized by the presence of somewhat sparsely scattered *polymorphous* cells, though other cells are present; hence this layer is frequently called "the layer of polymorphous cells." It is broken up into vertical columns by the bundles of vertical fibres, and its demarcation from the white matter below is somewhat indistinct owing to the fact that in the brain the white matter, especially that lying beneath the cortex, contains cells and small groups of cells lying between the bundles of fibres to a much greater extent than does the white matter of the spinal cord. The upper portion of this layer is the most usual situation for the Golgi cells with short branching axons.

The second layer (Fig. 131, II.), lying above the preceding, varies much more both in thickness (2 mm. to 1 mm.) and in its characters. It is marked in its lower part by a horizontal streak (Baillarger's band, Fig. 131 *z*) due to numerous, mostly fine, medullated fibres running horizontally. In the cortex of the Island of Reil, this horizontal layer is developed into a conspicuous sheet of medullated fibres, separating the third and second layers by a distinct interval of obvious white matter. The third layer, of polymorphous cells, thus detached from the rest of the cortex is what is called the *claustrum* (Figs. 119, 120, &c., *cl*).

The distinguishing feature of this second layer is the presence of the characteristic *pyramidal* cells; hence this layer is frequently called "the layer of pyramidal cells." The cells are usually scattered but are here and there gathered into small groups. Some of the cells are 'large pyramidal' cells, others 'small pyramidal' cells, and yet others of a size which may be called medium. The large cells are found in the lower part of the layer, and the small cells are most abundant in the upper part; hence the whole layer is sometimes divided into a lower layer, in most regions narrow (·65 mm. to ·10 mm.), of large, and an upper layer, in most regions wider (1·75 mm. to ·5 mm.), of small pyramidal cells, in which case the polymorphous layer is counted as a fourth layer, succeeded by a third and second. Others again would divide the whole pyramidal layer into three layers, the lowermost being characterized by the presence of large cells, the middle by that of medium sized cells, and the uppermost consisting exclusively of small cells, these being closely packed together; but any distinction which may be made between the different parts of the whole layer is far less obvious than the distinction between the layer as a whole, and either the polymorphous layer below and the layer above of which we have to speak; and it is best perhaps to consider it as one layer, *the* layer of pyramidal cells. The lower part of the layer, like the polymorphous layer below, is split up into columns by the medullary rays of vertically disposed fibres; but these medullary rays diminish upwards (or increase downwards), the constituent fibres spreading away from the ray into the columns of grey matter, so that in the upper part of the layer the rays are far less distinct. This dispersion of a medullary ray will readily be understood if it be remembered that the fibres constituting it are on the one hand the axons of pyramidal (and other) cells, on their way to the white matter, and on the other hand axons of cells in distant parts on their way to terminate by synapses in some part or other of the cortex. At about its middle the layer is marked by a second streak of horizontal fibres, Gennari's band (Fig. 131 *y*).

The first and most superficial layer (Fig. 131, I.), is characterized by the predominance of the molecular ground substance, the cells being few and far between, and hence is called the *molecular layer*. The ground substance itself seems to be more largely neuroglial in nature than in the other layers containing a large proportion of neuroglial cells, and, as we said above, its extreme surface appears to be furnished by neuroglia alone. Nevertheless the fibrils which traverse it and which give to sections of it the 'molecular' appearance are to a very large extent fibrils nervous in nature.

Many of these fibrils are either the dendrites or branching axons of the peculiar fusiform horizontally disposed cells which, as we have said, lie scattered in this area. But others, and indeed the majority, are on the one hand the terminations of the apical dendrites of the pyramidal cells, both large and small, and on the other hand the terminations of axons either of cells in the lower layer of the same cortex (cells of Martinotti with ascending axons) or of cells situate in other parts of the brain, the latter reaching the molecular layer after traversing the underlying parts of the cortex in the medullary rays, whose tapering summits may be traced into this layer. The molecular layer as a whole may in fact be considered as a dense mass of synapses. It is not however the molecular layer alone which is the seat of synapses; throughout its whole thickness the cortex may be regarded as an area of synapses. And this perhaps is its dominant feature; to this however we shall return.

§ 651. The general arrangement just described varies, as we have said, in different regions of the cerebral surface. We must content ourselves here with pointing out the characteristics of two or three important regions.

The region which we have (§ 632) called the 'motor area' or 'region,' is characterized on the one hand by the great thickness of the second layer, or layer of pyramidal cells, as well as by the number and size of the cells contained in it, and on the other hand and especially, by the prominence in its lower part of remarkable clusters of very large pyramidal cells, of the kind which are referred to above (§ 649) as being frequently called 'giant' or 'ganglionic' cells. Such cells are very common in the upper part of the precentral and at the summit of the postcentral convolution, and in the paracentral lobule, acquiring their greatest size at the top of the precentral convolution.

The occipital region is characterized by the prominence of the smallest pyramidal cells. These not only form in this region a distinct division of the lower depths of the second layer, below the larger pyramidal cells, but are also conspicuous at other depths, their arrangement being such that some authors have been led to divide the cortex of this region into seven or even eight layers. In the present state of our knowledge we may be content with insisting that the great mark of this occipital region is the abundance of these smallest pyramidal cells, whereby the larger pyramidal cells seem to be made less conspicuous. It is worthy of notice however that in the lower part of the second layer a few cells of very large size are met with, which by their large and numerous dendrites and conspicuous axon resemble the large pyramidal cells in the motor region; but it should be noted that while these large cells occur (at least in man and in the monkey, though not in some of the lower animals such as the rabbit) in very definite clusters in the motor region, they occur singly in the occipital region. In this occipital region the layer of horizontal fibres ('Gennari's band') in the second layer is very conspicuous, and owing to the number of ordinary medullated fibres present forms a white streak visible even to the naked eye.

In the frontal region, in front of the motor region, the arrangement is more in accordance with what we have described as the general plan. The layer of large pyramidal cells is much thinner than in the motor region, while the layer of polymorphous cells is thicker than elsewhere. Very small pyramidal cells are perhaps more abundant in this region throughout all layers than in the motor region, but are far less conspicuous than in the occipital region.

We may here remark that the transition in structure from one region to another is very gradual, not sharp and distinct, and is perhaps especially gradual in passing from the motor region backwards to the occipital region. It is not possible to recognize histologically the limit, for instance, of the motor region as determined experimentally.

In special regions of the brain, for instance in the olfactory bulb, of which we shall speak later on, very great modifications of the general plan may be observed in the cortex. We cannot enter upon these but may just refer to the cornu ammonis or hippocampus. At the ventral end of the temporal lobe, the gyrus hippocampi, the structure of whose cortex follows the general plan, is thrust inward so as to project into the cavity of the descending horn of the lateral ventricle, forming the ridge-like prominence known by the above name. The substance of the cornu ammonis is therefore cortical substance covered on the side of the ventricle by a thin prolongation of the central white matter, which is in turn covered by the ependyma lining the ventricle. A vertical section of this substance shews that while the polymorphous layer is reduced to small dimensions, the second layer, that of pyramidal cells, especially of the large ones, though narrow, is well developed. The cells are large and remarkably long; the apical dendrites are arranged so regularly as to give rise, especially in stained preparations, to a marked radiate appearance, and the basal dendrites are almost as well developed as the apical; in fact these cells are more richly supplied with dendrites than are any other known cells. The axon usually arises from the root of one of the basal dendrites. At the upper part of the second layer there occurs a large development of capillary blood vessels and a scarceness of cells, giving rise to a 'lacunar' appearance; and the first or molecular layer is of some considerable thickness.

§ 652. In attempting to review the salient features of the cerebral cortex we may perhaps repeat what we said above, namely, that it is essentially an area of multitudinous synapses. In speaking of the cerebellum we said that the cell of Purkinjé might be regarded as the keystone of an arch of manifold synapses; and perhaps, much in the same way, the pyramidal cell may in the cortex be looked upon as the keystone of synapses still more manifold and far more important. Assuming that in its ordinary labours the pyramidal cell sends impulses from itself along its axon, those impulses are the offspring, directly or indirectly, of other impulses breaking like waves on the spreading basal dendrites, on the lateral branches of the apical dendrite, and especially on the endings of the apical dendrite in the molecular layer. And these advehent impulses, whether they stir up to activity a previously quiescent cell, or modify a pre-existent, possibly in some cases a so-called automatic activity, may reach the cell from many sources. They may travel to it along the axon or the collateral of an axon, reaching the area of cortex in which the cell is placed from the underlying white matter, and as we have seen, passing into that white matter from different regions, from another district of the cortex of the same hemisphere, from the opposite hemisphere or from one or other of the various areas of grey matter in the other parts of the brain which send fibres to the cortex. Further, the impulses may reach the pyramidal cell along the axons of other cells in the cortex, for instance in the deeper parts along an axon of a cell of Martinotti, or along the branches of the axon of a cell of Golgi, and in the superficial molecular layer along the axon of a pluripolar cell. If, as some think, the axon of a polymorphous cell is not always directed to the underlying white matter but may, in certain cases at least, ascend and form synapses in the cortex, another channel for advehent impulses is disclosed. If we may assume, and we seem entitled to do so, that each single fibril into which an axon divides or which it gives off may carry an impulse of its own, the variety of ways in which even a single pyramidal cell may be affected, seeing how many fibrils and of what varied origin bear upon it, must be exceedingly great, and the consequent activity of the cell exceedingly varied.

Looking now at the pyramidal cell from another point of view, namely that of its axon, bearing in mind that the axon even if it does not divide along its course may bear numerous collaterals, we see that the cell may, by the endings of the trunk or of the collaterals, affect many different structures and produce very different effects. In this connection it is well to bear in mind that in some cases the collaterals which the axon gives off soon after leaving the cell run back into the cortex, and hence the impulse starting from a pyramidal cell may react on the very area of cortex from which it sprang.

The division of pyramidal cells into large, medium sized and small, does not appear a very satisfactory one. It may indeed be that all the pyramidal cells are alike as regards their intrinsic powers, and that the larger ones differ from the smaller ones only in that they are larger because they have to uphold and govern the nutrition of a longer stretch of axon. But it may also be, and perhaps we may say probably is the case, that apart from size the pyramidal cells do differ from each other, and that we may hereafter have to distinguish different kinds. If that be so, the potentialities of complexity are still greater.

Assuming the common opinion to be correct that the polymorphous cells send their axons into the white matter, thence to pass as white fibres to diverse destinations, we may regard these as a set of organs different from the pyramidal cells and played upon through synapses different from those proper to the pyramidal cells. If this be so, we hardly doubt but that the actions of the two sets are in some way or other coordinated. And, in relation to this, we may remark, repeating to a certain extent what we said in dealing with the spinal cord, that even making every allowance for diversity in the several cells of intrinsic powers determined by the innate qualities of cell substance, assuming that if two identical impulses impinge in the same manner on two pyramidal cells, or on a pyramidal cell and a polymorphous cell, the result will be different in the two cases, in consequence of the intrinsic nature of the cell, we may still conclude that the complexity of the manifestations of the cortex is also in large measure due to each cell being the nodal point of many possible lines of action, and so subject to numerous combinations of influences. We may add that each such nodal point is a unit in a system of nodal points, and each system may be in turn swayed by diverse impulses. In the play of multitudinous impulses, reaching it directly or indirectly from all parts of the rest of the nervous system and so from all parts of the body, more perhaps than in the molecular nature of its substance, lies the special prerogative of the cerebral cortex.

Lastly, we must remember that, as we have already urged, though much may be said for the assumption that in a nerve cell impulses usually pass along the axon from the perikaryon and along the dendrites to the perikaryon, we have no right to assume that impulses or influences never pass in the contrary direction. We have perhaps less right to assume this in the case of the nerve cells of the cortex than in the case of other nerve cells. And, if we reject the assumption and admit that an event started in the endings or along the course of an axon may influence in a backward direction the cell, including its dendrites, from which it springs, the significance of the multitudinous connections on which we have been dwelling becomes still more striking.

In this relation it may be worth while to call to mind the peculiar features of the growth of the brain, and especially of the cortex and its belongings. In one respect the brain of the infant is less mature than is any other part of the body, the structural development which it undergoes from birth to adult age is more marked than in other tissues. In another respect its growth throughout life is much more limited than that of other tissues. In other tissues old cells die, new ones taking their place, and loss by injury or disease is soon repaired by the formation of new but identical tissue. In the brain, and indeed in the whole central nervous system, this is not the case. A piece of the brain or of the spinal cord once lost, is lost for ever. Put in another way this means that after a certain epoch, and the epoch seems to be late intrauterine life or quite early infancy, the installation of the nerve cells of the central nervous system is complete, no more new cells are formed. The growth which follows this epoch consists exclusively in the development of the existing units, in the amplification and extension of dendrites and axons, and in the expansion of nuclei and perikaryons of cells already laid down, not in the addition of new units. And what is lost by the deprivation of acquiring new cells is made up for, perhaps more than made up for, by the remarkable power which the nerve cell possesses on the one hand of growing with the growth of the body, and on the other of repairing itself after injury, as seen in the section of nerves, the latter power being retained to the extreme limits of old age. Further, that dependence of growth on the stimulus of environment and circumstance, which is seen more or less obscurely in other tissues, as when the muscle strengthens by exercise, is conspicuous in the cerebral nerve cells. Shut off from all opportunity of reproducing itself and adding to its number by mitosis or otherwise, the nerve cell directs its pent up energy towards amplifying its connections with its fellows, in response to the events which stir it up. Hence it is capable of an education unknown to other tissues.

One of the more easily recognized tokens of the growth and development and the consequent full functional activity of a nerve cell is the deposition of medulla around, the myelination of, the axon and its branches; we may assume that an axon, so long as it has not acquired the medulla which is proper to it, though it may, like a non-medullated fibre, be capable of carrying impulses of a certain kind, is not in the full enjoyment of all its powers. This myelination is especially late in the cerebral hemisphere and continues to advance here long after it has ceased elsewhere. At birth no medullated fibres are present at all in the cortex itself, and the only part beneath the cortex, where the white matter is really white, that is, contains medullated fibres, is the motor area. We have seen that in the spinal cord the part which is the last to acquire its medulla is the pyramidal tract; but this, when it reaches the cerebral hemisphere, finds itself among fellows all later in this respect than itself with the exception of the fibres connected with the same area as itself but carrying impulses to instead of away from it; these afferent fibres as we have already said become myelinated a little earlier than the efferent fibres which constitute the pyramidal tract. We may look upon all the period antecedent to myelination as a period during which the growth of the axon, its extension and the putting forth of collaterals is going on actively, though not necessarily to cease with the completion of myelination; and in this respect it is worthy of notice that the region of the hemisphere which is the last in which the fibres put on their medulla, is the frontal region from which, as we shall see, rough experimental examination can elicit no definite response as it can in the parietal and even in the occipital region. Broadly speaking the 'projection' fibres both efferent and afferent, those which put the cortex in connection with lower parts of the brain, and so with the motor and sensory organs of the body, are myelinated first; the 'association' fibres, those which bring parts of the cortex itself into mutual connection, are all myelinated later. It is further worthy of notice that in man the whole of the motor area does not become medullated uniformly at the same time. Cores, so to speak, of medullated fibres make their appearance, each surrounded by a zone in which myelination takes place more tardily. This we may interpret as meaning that certain main connections between the cells in a special part of the cortex and distant structures are laid down first, and subsidiary connections established later; and it is open for us to suppose that these subsidiary connections are especially influenced by what we call education.

SEC. 7. ON VOLUNTARY MOVEMENTS.

§ 653. When we examine ourselves we recognize certain of our movements as 'voluntary'; we say that we carry them out by an effort of the 'will.' And when we witness the movements of other people or of animals we regard as also voluntary such of those movements as by their characters and by the circumstances of their occurrence seem to be carried out in the same way as our own voluntary movements. Even in the case of some of our own movements we are not always clear whether they are really voluntary or no; and in the case of other people and of animals it is still more difficult to decide the question. It would be out of place to attempt to discuss here how voluntary movements really differ from involuntary movements, or in other words, what is the nature of the will; we must be content to take a somewhat rough use of the words 'voluntary,' 'volitional,' and 'will' as a basis for physiological discussion. We may however remark that so far as the muscular side of the act, if we may use such an expression, is concerned, a voluntary movement does not differ in kind from an involuntary movement. It is perfectly true that a skilled man may by practice learn to execute muscular manœuvres which he would not have learnt to execute had not an intelligent volition been operative within him; but our own experience teaches us that many more or less intricate movements which have undoubtedly been learnt by help of the will may be carried out under circumstances of such a kind that we feel compelled to regard them as, at the time, involuntary; and it may at least be debated whether every movement which we can carry out, by an effort of the will, may not appear under appropriate circumstances as part of an involuntary act. In the case of the lower animals, in the frog deprived of its cerebral hemispheres for instance, we have seen that voluntary differ from involuntary movements, not by their essential nature but by the relation which their occurrence bears to circumstances. We have therefore to seek for the distinction between voluntary and involuntary, not in the manner in which the muscular and nervous components of a movement are co-ordinated, but in the nature of the process which starts the whole act.

The histories, related in a preceding section, of various animals deprived of their cerebral hemispheres, while they have further shewn the difficulty of drawing a sharp line between the presence and absence of volition, such as when we appeal to our own consciousness we seem able to draw, have taught us that in a broad sense the presence of volition is, in the higher vertebrata, dependent on the possession of the cerebral hemispheres; and we have now to inquire what we know concerning the way in which the cerebral cortex, for this, as we have seen, is the important part of the cerebral hemisphere, by the help of other parts of the nervous system carries out a voluntary movement.

§ **654**. With this view we may at once turn to the results of experimental interference with the cortex. When the surface of the brain is laid bare by removal of the skull and dura mater, mechanical stimulation of the cortex produces little or no effect, thus affording a contrast with the results of mechanically stimulating other portions of the brain, or other nervous structures. And for a long time the cortex was spoken of as insensible to stimulation. When, however, the electric current is employed, either the make and break of the constant current, or the more manageable interrupted current, very marked results follow. It is found that certain movements follow upon electric stimulation of certain regions or areas. The results, moreover, differ in different animals. It will be convenient to begin with the dog, on which animal the observations of this kind were first conducted.

When the surface of the dog's brain is viewed from the dorsal surface a short but deep sulcus is seen towards the front, running outwards almost at right angles from the great longitudinal fissure; this is called the *crucial sulcus* (Fig. 132), the gyrus or convolution in front and behind it, and sweeping round its end being called the *sigmoid gyrus*. It will hardly be profitable to discuss here either the homology of this sulcus or the names of the other sulci and convolutions of the dog's brain. We mention this sulcus because it is found that stimulation of the cortex in a region which may be broadly described as that of the neighbourhood of this crucial sulcus gives rise to movements of various parts of the body, whereas stimulation of other parts of the cortex either gives rise to no movements at all, or, if it does produce them, does so less certainly.

The region of the cortex in the neighbourhood of the crucial sulcus has therefore been termed an 'excitable' or 'motor' region. Stimulation of particular districts or areas of the region leads to particular movements carried out by particular muscles. For instance, stimulation of the more median parts of the gyrus behind the crucial sulcus (Fig. 132 ‡) leads to movements of the hind limb, whereas stimulation of the lateral part or outer end of the same gyrus leads to movements of the fore limb, and we may here distinguish between an area stimulation of which (Fig. 132 +)

leads to flexion of the fore limb, and an area (Fig. 132 ∓) stimulation of which leads to extension of the same limb. In a similar way stimulation of other areas within the 'motor' region leads to movements of this kind or of that kind of the tail, of the eyes, of the mouth, of other parts of the face, of the tongue, and so on. Obviously in the dog this region of the cortex has connections with the skeletal muscles which do not obtain between other regions of the cortex and those muscles; and further, the region in question is topographically differentiated, so that certain areas or districts of the region are specially connected with certain skeletal muscles or groups of muscles. We may speak of a 'localisation of function' in this region and in the several areas within the region as compared with each other.

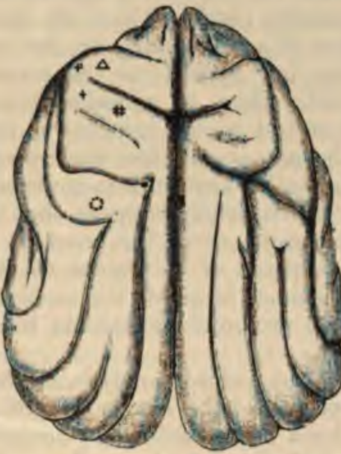

FIG. 132. THE AREAS OF THE CEREBRAL CONVOLUTIONS OF THE DOG, ACCORDING TO HITZIG AND FRITSCH.

(1) Δ The area for the muscles of the neck. (2) ∓ The area for the extension and adduction of the fore limb. (3) + The area for the flexion and rotation of the fore limb. (4) ‡‡ The area for the hind limb. Running transversely towards and separating (1) and (2) from (3) and (4) is seen the *crucial sulcus*. (5) ○ The facial area.

The muscles which are thus thrown into contraction are the muscles of the opposite side of the body. When 'the fore limb area,' as we may call it, of the right hemisphere is stimulated, it is the left fore limb which is moved; and so with the other areas; it is only in exceptional cases, as in certain movements of the eyes, that the effect is bilateral; a movement confined to the same side as that stimulated is never witnessed.

The results are most clear when the current employed as a stimulus is not stronger than is just sufficient to produce the appropriate movement (roughly speaking a current just perceptible to the tongue of the operator is in ordinary cases a useful one), and when the cortex is in good nutritive condition. In any experiment the results obtained by the earlier stimulations, soon after the cortex has been exposed, are the more precise; after repeated stimulations the surface is apt to become hyperæmic, and it is then frequently observed that the movements resulting from the stimulation of a particular area are not confined to the appropriate muscles, but spread to the corresponding muscles of the opposite side, then to muscles connected with other cortical areas, and at last to the muscles of the body generally; at the same time the movements lose their distinctive purposeful character and the animal is thrown into convulsions of an epileptiform kind. It not unfrequently happens that an experiment has to be stopped in consequence of the onset of these epileptiform convulsions. The response of movement to stimulation may be observed while the animal is under the moderate influence of an anæsthetic, but a too profound anæsthesia lessens or annuls the effects.

In order to carry out a closer analysis of the phenomena it is desirable to watch or record the contraction of a particular group of muscles, or perhaps better still a particular muscle, *e. gr.* the area for extension of the hind limb may be studied by help of the extensor digitorum communis of the limb. When this is done the following important facts may be observed. The area of cortex having been found which gives the best movements, and the stimulus being no stronger than is necessary, isolation of the area from its lateral surroundings by a circular incision carried to some little depth will not prevent the development of contractions in the muscle; but these do cease, even without the circular incision, if by a horizontal section the grey cortex is separated from the subjacent white matter. After removal of the cortex, stimulation of the white matter underlying the area produces the appropriate contraction; not only however is a stronger stimulus necessary, but also the latent period, that is, the time intervening between the beginning of the application of the stimulating current and the beginning of the muscular contraction is appreciably shortened. The appropriate contractions not only appear when the white matter immediately below the cortex is stimulated, but by making successive horizontal sections and stimulating each in turn, the effect may, so to speak, be traced through the central white matter of the hemisphere down to the internal capsule. We may conclude from these results, that when the current is applied to the surface of the cortex, certain parts of certain structures in the grey matter are stimulated, the process having a marked latent period, and that as the outcome of the changes induced in the grey matter, impulses pass along the fibres leading down from the grey matter to the internal capsule and so by the pedal system of fibres to the spinal cord and motor spinal roots. The anatomical considerations advanced in a previous section lead us to suppose that the fibres in question belong to the pyramidal tract, on which we have so much insisted; and as we shall see all our knowledge confirms this view.

It must not, however, be supposed that the several areas stimulation of which produces each its distinctive movement, are in the dog sharply defined from each other; when the term area for extension of the hind limb is used it must not be supposed that the area can be defined by an outline, within which stimulation produces nothing but extension of the hind limb, and outside which stimulation never produces extension of the hind limb. All that is meant is that extension of the hind limb is the salient and striking result of stimulating the area. When we study the various movements, and especially perhaps when we study, by help of a graphic record, the contractions of various individual muscles resulting from the stimulation of various parts of the motor region, we find not only that the areas for particular movements or particular muscles are very diffuse, but that the several areas largely overlap each other. If for instance we were to map out on the same diagram the several areas belonging to four or five muscles of different parts of the body, such as the extensors of the digits of the fore and of the hind limb, the flexors of the same, and the orbicular muscle of the eyelid, that is to say, the several areas within which in turn stimulation of the cortex produced contraction of the particular muscle, the overlapping would be so great that the whole figure would appear highly confused. In a similar way the excitable motor region as a whole would gradually merge into, be broken up into, the unexcitable frontal, occipital and temporal regions, in front, behind and below. In other words, the localisation in the cortex of the dog is to a marked degree imperfect.

In this respect the dog, corresponding to its position in the animal hierarchy, is intermediate between such animals as the rabbit, the bird, and the frog, on the one hand, and the more highly developed monkey on the other; and that is one reason why we have taken the dog first and dwelt so long upon it. In the rabbit, a similar localisation may be observed, but much less definite, much more diffuse. In birds, electrical excitation does in some species produce certain limited movements, especially of the eyes and head; in other species no effect at all can be observed. In reptiles, amphibia and fishes no good evidence has been obtained that electrical stimulation of the cerebral hemispheres will produce movements. It will not be profitable to dwell on the details of these lower animals; but the phenomena of the monkey, leading up as they do to those of man, call for special notice.

§ **655**. When in a monkey, in an individual for instance belonging to the genus *Macacus*, the surface of the cerebrum is explored with reference to the effects of electric stimulation, it is found that when the current is applied to the precentral or ascending frontal and the post-central or ascending parietal convolutions which lie respectively in front of and behind the important central fissure or fissure of Rolando (cf. Fig. 133), movements of the fore limb follow. The 'area for the fore limb' thus discovered is more circumscribed and definite than is the corresponding area in the dog. Its outline (Fig. 134) is roughly that of a truncated triangle bisected by the central fissure, with the broad base at some distance from the mesial line, and the truncated apex reaching on the lateral surface of the hemisphere to a well-marked bend in the lower part of the central fissure. Behind, it reaches as far as the intra-parietal fissure, which somewhat sharply defines its hind border, and in front it ceases no

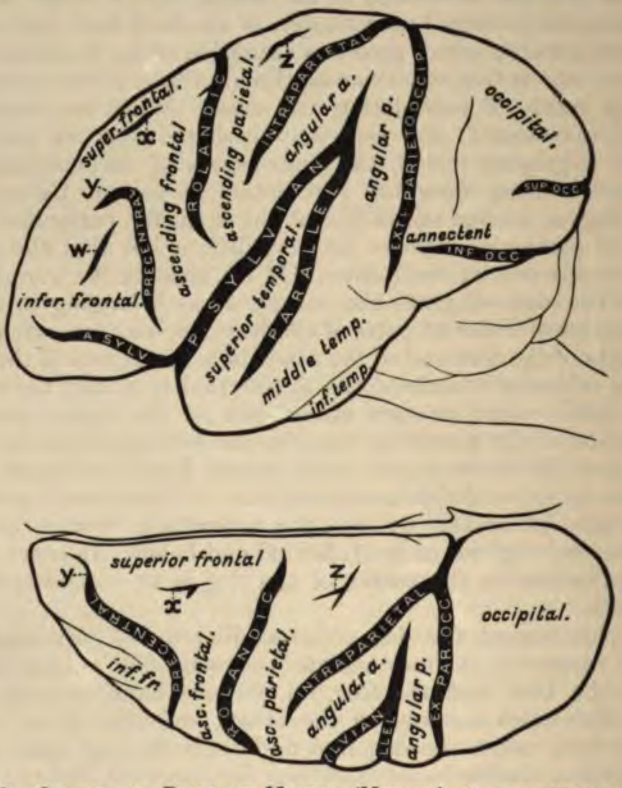

Fig. 133. Outline of Brain of Monkey (Macacus) to shew principal Sulci (Fissures) and Gyri (Convolutions). (Natural size.)

The brain figured is the same as that in Fig. 134, and the two figures should be consulted together. Over each sulcus, purposely printed very thick, the name is written in *small capitals*, over each gyrus in *italics*. x indicates the small depression, hardly to be called a sulcus, which is supposed to be homologous with the superior frontal sulcus of man; and w, y, z similarly indicate sulci whose homologies are not certain. For some synonyms see Figs. 137, 138.

less definitely at some little distance behind the precentral fissure. Further examination shews that the whole area is divided into areas corresponding to movements of particular parts of the fore arm, and that these are arranged in a definite relation to each other. In the more dorsal part of the area, at the base of the triangle, stimulation produces movements of the shoulder (Fig. 134); if the electrodes be shifted ventrally movements of the elbow make their appearance; if still more ventrally, movements of the wrist come in, and these are in turn succeeded ventrally by movements of the digits generally, of the forefinger, and lastly of the thumb. A very striking experiment may at times be made; when a current of suitable strength is applied, first at the

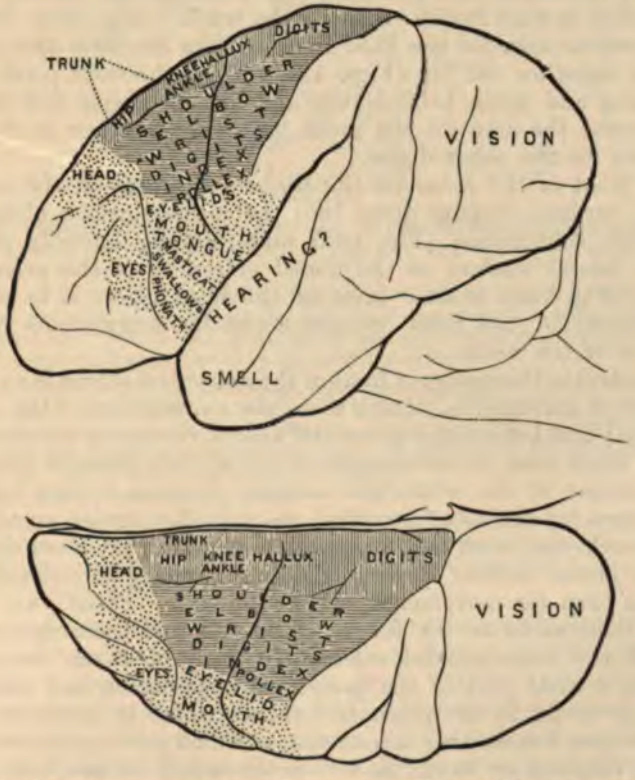

FIG. 134. LEFT HEMISPHERE OF THE CEREBRUM OF MACACUS MONKEY VIEWED FROM ITS LEFT SIDE, AND FROM ABOVE. (Natural size.)

The figure shews the positions of the portions of the cortex concerned with movement of various parts, and with the senses of sight, smell, and hearing. The cortical area connected with the movements of the leg is shaded vertically across, that with the movements of the arm horizontally, and that with the movements of the trunk in a slanting direction; the area connected with movements of the head (neck), face, and eyes is dotted. The course of the chief fissures is indicated by single lines.

lower, ventral border of the area, and then gradually advanced upwards towards the mesial line, the thumb first is seen to move, then the forefinger, then the rest of the digits, then the wrist, next the elbow, and lastly the shoulder; the movements however are very apt to merge one into the other. Further, in certain parts of the area the predominant resulting movement is flexion of the appropriate segment of the limb, in other parts extension, in certain parts abduction, in other parts adduction, and so on.

Similar exploration shews that the "area for the hind limb" lies on the median side of the area for the fore limb, stretching besides on to the mesial surface along the marginal convolution which forms the dorsal portion of the wall of the great longitudinal fissure; it reaches as far back as the intra-parietal sulcus, and is succeeded in front by the "area for the trunk" (Fig. 135). Within this general area for the hind limb we may similarly distinguish special areas for the hip (Figs. 134, 135) in the front portion, for the knee and ankle behind this, and for the digits still farther backwards, the area for the great toe being however in front of the area for the other digits.

In front of the areas for the limbs and trunk, on the median dorsal surface, dipping down into the mesial surface along the marginal convolution (Fig. 135) and reaching laterally on the dorsal lateral surface to the dorsal extremity of the precentral sulcus (Fig. 134), is the "area for the head," that is to say, for movements of the head brought about by contractions of the muscles of the neck.

Ventral to this again, in front of the precentral sulcus is an "area for the eye movements," that is to say, for contractions of the ocular muscles; and behind the precentral sulcus, ventral to the arm area, lies a small area for movements of the eyelids, brought about by contractions of the orbicularis muscle. Ventral to this again is the "area for the face," in which we may distinguish an area for the mouth, that is an area stimulation of which produces changes in the buccal orifice, opening, shutting, drawing to one side &c., and an area for movements of the tongue. These two areas reach downwards to the fissure of Sylvius, and backwards to the line of the intra-parietal sulcus. In front of them, occupying all the ventral part of the precentral convolution and reaching forwards as far as the precentral sulcus, where it meets the area for the eyes, lies an area stimulation of which produces movements of the pharynx or larynx as well as the mouth or face, and which may be divided into areas for mastication, for swallowing, and for the production of the voice.

We might speak of these several areas in another way by referring to the nerves concerned in carrying out the several movements, though in doing so we must remember that there is not an exact correspondence between the relative position of a muscle along the axis of the body or along the axis of a limb and the relative position along the cerebrospinal axis of the nerve or nerves governing the muscle. We may however, adopting this method, note that the sacral and lumbar nerves are represented by the most mesial portion of the whole motor area and by the hind division of this mesial portion; that the lumbar and thoracic nerves are represented by the front division of the same mesial portion; that the upper thoracic with the lower cervical nerves belong to a region lying lateral to, and the upper cervical nerves to one lying in front of the preceding area; and lastly that the remaining lateral and ventral portions of the whole motor region appertain to the cranial nerves. But the topographical differentiation does not come out so clearly by this method, as by that of taking for our guide distinctive movements of the several parts of the body.

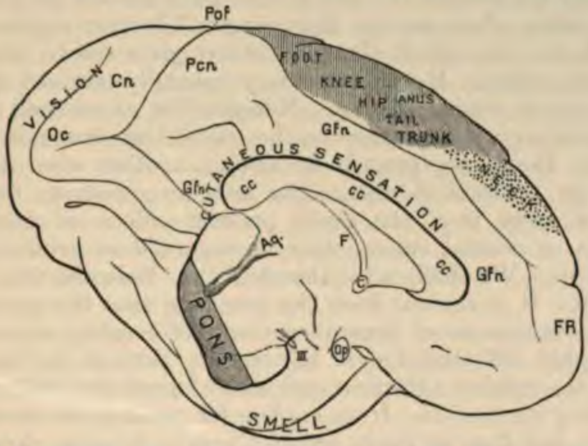

FIG. 135. MESIAL ASPECT OF THE LEFT HALF OF THE BRAIN OF MACACUS, DISPLAYED BY SECTION IN THE MEDIAN SAGITTAL PLANE AND REMOVAL OF THE CEREBELLUM. (Natural size.)

The hatched and stippled parts of the surface shew the regions of the cortex connected with movements of the *foot*, *knee*, *anus*, *hip*, *tail*, *trunk*, and *neck* respectively. The several positions of the areas of cortex connected with *vision* and *smell* are indicated by the appropriate words.

The plane of section has passed through the corpus callosum, *cc*, *cc*, *cc*, and through the anterior commissure, *c*, sparing the left pillar of the fornix, *F*; behind it has bisected the anterior part of the pons, laying open the aqueduct, *Aq*. (iter a tertio ad quartum ventriculum). *Pons*, the left half of the pons in frontal section. *Op*. the optic commissure cut across.

III. the root of the third cranial nerve.

FR. the frontal pole, *OC*. the occipital pole; *Cn*. the cuneus, *Pcn*. the precuneus; *G. fn. G. fn. G. fn.* the gyrus fornicatus; the unlettered fissure seen to form the upper boundary of this gyrus in its supra-callosal part is the calloso-marginal, *Po. f.* the parieto-occipital fissure.

It will be observed that all these areas taken together, represented by the portion of Figs. 134, 135 shaded in one way or another, occupy chiefly the parietal region of the cerebral surface though they also reach into the frontal region. Stimulation of the frontal region in front of this area or of the occipital and temporal regions behind may, as we said, give rise to movements of certain parts; but as we have also said such movements present characters of their own and must be considered by themselves. Their occurrence does not remove the strong contrast presented by the region of the cortex which we are discussing to all other regions. This region is the one which above all others gives rise to movements when stimulated. Hence it has very naturally received the name of the 'motor' region or area. Nevertheless, as we shall see later on, there are grave objections to the use of this term; it is apt to mislead. Hence we propose to employ another word and shall choose an anatomical one. The area in question, though it stretches away from the great primary sulcus or fissure, the Rolandic or central sulcus, may be regarded as centered round that sulcus. We shall call it therefore the 'Rolandic area.'

§ 656. It is obvious from the foregoing that the mechanisms for the development of these movements of cerebral origin are far more highly differentiated in the monkey than in the dog. But even in the monkey (Macacus and allied forms) the differentiation is still very incomplete. If we explore for instance the area for the wrist we find that its limits are ill-defined. In some parts of the area we obtain movements of the wrist only, but in other parts of the area stimulation produces not only movements of the wrist, but also of the shoulder or of the digits, or of the neck; and so with the other areas.

If, however, not a Macacus or other ordinary monkey, but the more highly developed ourang otang be taken as the subject of experiments, the differentiation is found to be distinctly advanced; the several areas are more sharply defined, and what is important to note, the respective areas tend to be separated from each by portions of cortex, stimulation of which gives rise to no movement at all.

The opportunities of stimulating the cortex of man himself have been few and far between, and have for the most part been conducted under unfavourable circumstances; but so far as the results thus obtained go, they shew that the topographical distribution of areas for the several movements is carried out on the same plan as in the monkey (we are purposely confining ourselves now to the results of artificial stimulation); and, moreover, justify the conclusion, which *a priori* reasons would lead us to adopt, that in man the differentiation is advanced still farther than in the monkey.

Thus when we survey a series of brains in succession, we find that while below the mammal a connection between stimulation of the surface of the cerebral hemispheres and skeletal movement is absent or uncertain, in the mammalian series as we pass from the rabbit, through the dog, and other lower mammals up to the monkey, the anthropoid ape, and so to man himself, an increasing differentiation of the cerebral cortex obtains, by which certain areas of the cortex are brought into special connection with certain skeletal or other muscles in such a way that stimulation of a particular portion of the grey matter gives rise to a particular movement and to that alone.

§ **657.** In treating of the structure of the brain we spoke (§ 632) of the pyramidal tract as starting from the parietal region of the cortex; and it is obvious that the fibres of this tract must be concerned in the development of the movements which we have just described. When the movements are brought about by stimulation of the fibres in some part of their course, in the internal capsule for instance, there can be no doubt that the stimulation starts impulses which, travelling down the tract to the origins of certain cranial or spinal nerves, in some way give rise to coordinate motor impulses along the motor fibres of the nerves; and we may with reason speak of the impulses then passing along the tract as motor or efferent in nature. When the stimulus is applied direct to the cortex, we may assume that processes, started in the grey matter, eventuate in similar efferent impulses along the fibres of the tract. All the evidence leads us to regard this tract as an efferent tract.

When the spinal cord is divided in the lower dorsal region and the electrodes of an electrometer are brought into connection with the transverse cut surface and with some point of the longitudinal surface above, the electrometer gives evidence of currents of action (manifested as negative variations of a demarcation current or current of rest, § 67) whenever the area of the hind limb is stimulated, but not when other parts of the cortex are stimulated. We have already said that stimulation of any part of the "motor" region may under abnormal conditions give rise to general epileptiform convulsions; when these occur during such an experiment as the above, currents of action manifest themselves in the lower dorsal cord, whether the stimulation giving rise to the convulsions be applied to the area for the hind limb or to any part of the motor region. It has been further observed that the currents of action developed within the spinal cord tally in a very exact manner with the muscular movements. The convulsions begin with a sustained 'tonic' contraction of the muscles, and the electrometer shews a similar sustained current of action; this is followed by rhythmic movements of the muscles, accompanied by corresponding rhythmic movements of the mercury of the electrometer. Without insisting too much on the exact interpretation of these results we may take them as at least shewing that, when the Rolandic region of the cortex is excited, nervous impulses accompanied by "currents of action" pass downward along the fibres of the pyramidal tract.

The results of stimulating the fibres of the tract in their course through the corona radiata and the internal capsule, and the results obtained by studying the degenerations following upon injury to or removal of the several parts of the cortical Rolandic area, agree in marking out the paths taken by the several constituents of the tract through the central white matter of the hemisphere, the corona radiata and the capsule. Comparing Figs. 134, 135 with Figs. 125, 126 and 127 it will be seen that the portion of the tract destined for the cranial nerves, and so for the movements of the eyes, the mouth, face, tongue, pharynx and larynx, starting from the ventral parts of the more frontal district of the Rolandic area, take up their position at the knee of the internal capsule; and the portion destined for those upper cervical nerves which carry out movements of the head through the muscles of the neck, starting from the extreme frontal and dorsal parts of the area, is also apparently directed to the knee of the capsule. The rest of the tract, starting from the part of the area lying at once behind and mesial to the above, occupies in the capsule a position posterior to them in the hind limb of the capsule; and it will be observed that the tract for the fore limb which begins on the surface lateral of the tracts for the trunk and hind limb, shifts its course in relation to theirs, so that in the capsule it is in front of them, not lateral to them. It may further be observed that while in the tracts for the trunk and hind limb the same fore and aft order which obtains on the surface is reproduced in the capsule, even apparently to the strange precedence of the ankle over the knee, the order of the several elements in the fore limb tract which is lateral on the surface becomes regularly fore and aft in the capsule. In the capsule the several elements are arranged in a lineal order, corresponding broadly to that of the distribution of the muscles along the longitudinal axis of the body; on the cortex they are disposed in an order the cause of which is at present not very clear, but which is probably determined by the respective relations of the several parts of the Rolandic area to the functional activity of the other parts of the cortex. In the shifting from the one order to the other, the several constituent fibres, as we have said, describe a somewhat peculiar course; and when we remember, as stated in § 632, that the order shewn in Fig. 125 is only the order obtaining at one particular level of the capsule, and that from the dorsal beginnings of the capsule in the corona radiata to its ventral end in the pes, the capsule is continually changing in form, and its fibres therefore continually shifting their relations to each other, the whole course of the several fibres of the tract from their origin in the cortex until they are gathered up into the central portion of the pes (Fig. 118 *Py*) must be a very complicated one.

When the area of one hemisphere is stimulated, the movement which results is in most cases seen on the other side of the body, and on that other side alone. Thus when the area for the fore limb is stimulated on the left hemisphere it is the right fore limb which is moved. This is in accordance with what we have learnt of the pyramidal tract and its ultimate decussation before it reaches the motor nerves, the decussation either occurring massively as in the case of the crossed pyramidal tract, or in a more scattered manner along the upper part of the spinal cord in the case of the direct pyramidal tract; and, as we have seen, there is a similar decussation for such part of the pyramidal tract as is connected with the cranial nerves above the decussation of the pyramids. Except in the case of certain areas for movements naturally bilateral of which we shall speak presently, the movement is normally on the crossed side, and on the crossed side only. Under abnormal conditions however the limb of the other side, that is of the same side as the hemisphere stimulated, may move also. But such an abnormal movement of the same side has not the same characters as the proper movement of the crossed limb. Instead of being an orderly coordinate movement, it is a more simple, either tetanic or perhaps tonic, or rhythmic, clonic, contraction of the muscles; it is also much more apt to be a movement of extension than of flexion. Obviously its mechanism is of a different nature from that by which the proper movement of the crossed limb is effected; but it is important to bear in mind that a movement of the uncrossed limb may take place; and further that, the abnormal conditions continuing, similar movements of an uncoordinated character may spread to the hind limb and other parts of the crossed side, though the stimulation be still confined to the arm area, then to other parts of the uncrossed side, until as we have said the whole body is thrown into epileptiform convulsions. This feature must not be forgotten. In fact it may be fairly insisted upon that while we may speak of a particular coordinate movement as being the normal outcome of an ordinary careful stimulation of a particular area in a normal condition, it is no less true that diffuse uncoordinated movements, culminating in general epileptiform convulsions, are the natural outcome of the stimulation of any area in an abnormal condition. And in attempting to form any opinion of the nature of the first act, we must bear the second in mind.

As we said above, the movements resulting from cortical stimulation are most conveniently described in terms of parts of the body, of the arm, of the thumb, of the tongue, &c. The movements of the same part may be further distinguished by means of the nomenclature usually adopted in speaking of muscular movements, such as flexion, extension, abduction, adduction, &c.; so that, within the area bearing the name of some particular part, such as the wrist for instance, we may perhaps distinguish the parts where the effects of stimulation are those of flexion from the parts where the effects are those of extension of that joint; and in like manner in reference to other parts. But it will be readily understood that it is easier to map out the area for a particular part than to distinguish areas corresponding to the several movements of that part. Hence the nomenclature usually adopted in speaking of the Rolandic area is one based on the parts of the body moved rather than on the character of the movements. The more closely however the movements in question are studied, the more probable it appears that the localisation which obtains in the cortex is essentially a localisation corresponding not to parts of the body, or to nerves, or to muscles, but to movements. In considering this point it must be remembered how rude and barbarous a method of stimulation is that of applying electrodes to the surface of the grey matter compared with the natural stimulation which takes place during cerebral action; the one probably is about as much like the other, as is striking the keys of a piano at a distance with a broomstick to the execution of a skilled musician. Were it in our power to stimulate the cortex in any way at all approaching the natural method, we should in all probability arrive at two results; on the one hand we should be able to produce at will a variety of movements of different degrees of complexity, some very simple, others very complex, and for these we should have to use names suggested by the characters and purpose of each movement, and by these alone; on the other hand we should find very decided limits to the number and kind of movements which we could evoke, limits fixed in the case of each subject partly by inherited organisation, partly by the training of the individual.

Some such results of refined experimentation are indeed already foreshadowed by the rude results of our present rough methods. The movements which usually follow stimulation of the Rolandic area, and which we have described as flexion, &c., are, so to speak, the elementary factors of ordinary bodily movements, the detached and imperfect chords of a musical piece; and in the following facts relating to their production we can recognize the influences of organisation and habit. As we have said, stimulation of the Rolandic area of one hemisphere produces movements, as a rule, which are limited to one side of the body, and that the opposite side. Now both in ourselves and in the higher animals a large number of bodily movements, especially of the limbs, are habitually unilateral; and, putting aside the question why there should be two halves of the brain, and why the one half of the brain should be associated with the cross half of the body, we may recognize in the unilateral crossed movement resulting from stimulation of the cortex in accordance with natural habits. But some movements of the body are ordinarily bilateral; the two eyes, for instance, are ordinarily moved together, and the two sides of the trunk move together very much more frequently than do the two fore limbs or the two hind limbs. And in accordance with this we find that stimulation of the area for the eyes on either hemisphere produces movements of both eyes, and stimulation of the trunk area of one hemisphere is also very apt to produce bilateral action of the trunk muscles; in such instances the movements on both sides are quite normal movements. We may incidentally remark that removal of the trunk area leads to a good deal of bilateral degeneration, that is, to degeneration of strands in the pyramidal tracts of both sides, whereas such a bilateral degeneration is comparatively scanty after removal of the leg or arm or especially of the thumb area.

That it is the movement and not the part moved which is, so to speak, represented on the cortex is further indicated by the relative magnitudes of the several cortical areas when they are mapped out according to parts of the body. The area for the arm, for instance, cf. Figs. 134, 135, is, so to speak, enormous compared to that of the trunk when the relative bulks of these two parts of the body are considered; and within the arm area itself the space occupied by the thumb and fore-finger and digits is, bulk for bulk, out of proportion to the space allotted to the shoulder; so also the area for the eyes or for the mouth is out of proportion to the size of those organs. But these relative sizes of the respective areas become intelligible when we bear in mind relative mobility, nimbleness and delicacy of execution; in these respects the shoulder is far behind the thumb, while the eyes and mouth surpass most other parts of the body.

We are brought yet a step further when we compare, in respect of the cortical Rolandic area, animals of different grades of organisation; and the results thus obtained lead us to the conclusion that the area is correlated not to movements in general, but to movements of a particular kind. Taking in series the rabbit, the dog, the monkey and man, we find in passing from one to the other an increase in prominence and in differentiation of the area accompanied by an increase in the bulk of the pyramidal tract; among the many striking differences between the brains of these several animals, these two features, the increasing complexity of the Rolandic area, and the increasing size of the pyramidal tract, are among the most striking. We may add that in animals below the mammals the pyramidal tract is wholly wanting. The size of the pyramidal tract is itself correlated to the complexity of the area, and, being the more easily determined, may be used as indicating both; the difference in the size of the pyramidal tract in these animals is seen all along the whole length of the cord (Fig. 136). Now as regards mere quantity of movement, if we may use such an expression, the differences between these animals are of no great moment. If we were to take the amount of energy expended as movement in twenty-four hours per gramme of muscle present in the body in each of the four cases, we should certainly not find any correspondence between that and the size of the pyramidal tract. If however we take a particular kind of movement, what we may perhaps call skilled movement, that is movement carried out by means of intricate changes in the central nervous system, we do find a remarkable parallelism in the above cases between the amount of such skilled movement entering into the daily life of the individual and the size of the pyramidal tract. In these two respects man is much above the monkey, and the monkey far above the dog. We may conclude then that the Rolandic area is in some way especially concerned with the kind of movement which we have called 'skilled.'

§ **658**. These skilled movements are to a large extent, though not exclusively, voluntary movements. We have in a previous section seen reason to believe that the cerebral cortex is in some way especially associated with the development of voluntary movements. Putting together this conclusion and the conclusions just arrived at we are naturally led to the further conclusion that the Rolandic area, with the pyramidal tract belonging to it, plays an important part in carrying out voluntary movements.

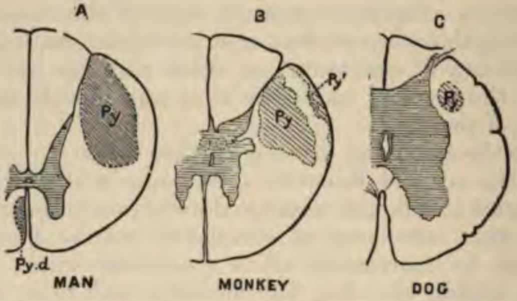

Fig. 136. Diagram to illustrate the Relative Size of the Pyramidal Tract in the Dog, Monkey and Man. (Sherrington.)

The figure shews in outline the lateral half of the cord, at the level of the fifth thoracic nerve, in *A*. Man, *B*. Monkey, *C*. Dog; *A* is a reproduction of D^5 in Fig. 107; *B* and *C* are drawn of the same size as *A*. *Py*., shaded obliquely, the pyramidal tract; the depth of shading indicates that the tract is more crowded with true pyramidal fibres as well as larger in *A* than in *B*, and in *B* than in *C*. In *B*, *Py'* is an outlying portion of the pyramidal tract separated from the rest by the cerebellar tract. *Py.d*. the direct pyramidal tract, present in man only. The grey matter seems relatively large in *C* because the section was taken from a very young puppy.

Do other facts support this view, and if so, what light do they throw on the question as to what part and what kind of part the motor region thus plays?

In this connection we naturally desire to know what are the results of removing from an otherwise intact animal the whole Rolandic area of the cortex, and more especially this or that particular portion of it. Before proceeding further, however, we may once more call attention to the caution given in § 582, and repeated in § 640; indeed when we consider the high organisation and complex functions which obviously belong to the cortex, when we bear in mind that it appears to govern, and must therefore be bound by close ties to almost all the rest of the central nervous system, we must be prepared to find after removing a portion of cortex that the pure 'deficiency' phenomena, those which result from the mere absence of a piece of the cortex, are largely obscured by the other effects of the operation.

In the rabbit the results have been almost purely negative. When in this animal the part of the cortex which may be considered as the motor region is removed, nothing remarkable is observed in the movements of the animal. We can hardly suppose that the operations of the central nervous system are exactly the same in an operated as in an intact animal, and the differences induced ought to be betrayed by the movements of the body; but at present they have escaped observation.

In the dog the removal of an area is followed by a loss or diminution of voluntary movement in the corresponding part of the body. When, for instance, the area for the fore limb is removed from the left hemisphere, the right fore limb is completely or partially 'paralysed.' In carrying out its ordinary movements the operated animal makes little or no use of its right fore limb. But this state of things is temporary only. After a while the animal regains power over the limb, and in successful cases recovery is so complete that it is impossible or at least very difficult to point out in the limb any appreciable deviation from the normal use. And careful examination after death has shewn not only that the area had been wholly removed, but also that there was no regeneration of the lost parts; the removal of the cortex leads in such cases, as usual, to degeneration of the corresponding strand in the pyramidal tract right away from the cerebral surface to the endings of the strand in the cervical and dorsal spinal cord. Nor can it be urged in such cases that diffused remnants of the arm area had been left in the remaining parts of the Rolandic area; for the whole of the area has been removed, and yet the animal has recovered to such an extent that at all events a casual observer could detect no differences between the movements of the two sides of the body. Nor can it be urged that, in such a case, where one side is removed, the remaining hemisphere takes on double functions; for the greater part of the Rolandic areas have been removed on both sides, and yet the animal's movements have been so far apparently complete that a casual observer would see nothing strange in them. Again, the whole Rolandic area has been removed from one hemisphere in a young puppy, and some time later when the movements seemed to have recovered their normal condition, the removal of the whole area of the other hemisphere has produced merely a paralysis of the crossed side of the body, and that as before only of a temporary character.

Two things have to be noted here. In the first place the removal of an area does affect the movements which are brought about by stimulating that area, it leads to their disappearance or at least to great diminution of them. In the second place, the physiological effect is temporary only, though the anatomical results of the operation are permanent, for the cortex is never renewed, and the pyramidal tract degenerates along its whole length, never to be restored; this shews that we have to deal here with events of a very complex character. When a particular movement results from stimulation of the appropriate cortical area, we may be sure that whatever takes place in the cortex and along the pyramidal tract, motor impulses, duly coordinated, pass along certain ventral roots to certain muscles; and we know that if we removed a sufficient length of each of those ventral roots that particular movement would be lost for the rest of the life of the individual. We may therefore infer that the events which, whatever be their exact nature, taking place in the cortex and along the pyramidal tract lead ultimately to the issue of motor impulses along the ventral roots, differ essentially from the events attending the transmission of ordinary motor impulses.

More instructive however than the study of the dog is that of the monkey, in which the movements being more varied and the proportion of skilled movements greater, it is easier to detect slighter defects. In the monkey as in the dog the removal of a cortical area is immediately followed by paralysis; if for instance the arm area be removed the arm seems helpless; the animal uses the arm very little and the hand hardly or not at all, the defect in power being most marked in the thumb and fingers and less so upwards to the shoulder. Other defects than those of movement are also observed, but of these we shall speak later on. We may however mention that not only is voluntary power interfered with by the operation, but also other uses of the muscle, and indeed even skeletal tone is affected; the limb hangs flaccid from the shoulder.

After a while the symptoms improve, the animal regains greater and greater power over the limb but the recovery is not complete. The finer, more skilled movements, those especially in which the thumb and fingers and the hand are concerned, are wanting or executed clumsily, and the movements best carried out are those in which the limb is used in combination with other parts, as for instance in progression. Reflex movements of the limb can be easily evoked, and tone returns or even becomes exaggerated as shewn by a more than usually brisk knee-jerk.

But, at all events in a large number of cases, this improvement ultimately gives way to a relapse. The movements of the limb become again more difficult, and this appears to be due to an exaggerated tone of the muscles giving rise to a rigidity (cf. § 599) especially of the flexors, the fingers and elbow becoming bent.

Corresponding results are obtained when other cortical areas are removed, the effects being most marked as regards the movements of those parts, such as the extremities of the limbs the cortical areas of which have the larger dimensions.

We have here obviously to deal with very complex events, justifying the caution given a little while back; but we may probably draw the following conclusions. While in the case of certain movements, the loss complete or partial which follows immediately after the operation is wholly recovered from, in the case of certain other movements there is no recovery, the loss is permanent. These latter movements belong to the class which we have called and may for the present continue to call 'skilled.' Some of these lost skilled movements are compensated for, in the sense that the end of the movement is gained by a new manœuvre, often involving unwonted muscles; but the actual movement is not regained. The temporary loss we may explain by appealing to that interference with the nervous machinery which we denote by the general phrase "shock"; the permanent loss is due to the loss of the cortical area and the contingent portion of the pyramidal tract. That is to say, the cortical area with its belonging pyramidal fibres is used for certain special skilled movements, and when it is wanting they are lacking too, however much the deficiency may be made up in other ways.

The deterioration which sets in later on is more difficult to explain. We must not dwell on it at any length but we call attention to it because it seems to point to a matter on which we have already said something and to which we shall have to return, namely, the dependence of the nutritive integrity of nervous elements on functional activity. The trophic degeneration of the pyramidal fibres which follows their separation from their trophic centres in the cortex reaches to the tips of their endings in the ventral horns of the spinal cord but no further. The mere trophic influences which determine the degeneration of the severed pyramidal fibre are not carried on to the cells of the ventral horn with which the fibre makes synapses and the axons of which govern the skeletal muscles. Nevertheless, though distinct trophic influences are not brought into play, the late rigidity and the at least apparent defect of power of which we spoke above, indicate that these cells, or to be more exact the nervous mechanisms of which the cells form a part are not in good working order. They are at least not working as usual, though all the circumstances of their life remain the same save and except the play upon them of influences from the endings of the pyramidal fibres. The absence of these influences throws them out of gear. And the fact that the deterioration in question though common in the monkey is not witnessed in the dog may be taken as shewing how in the former animal the life of the cells in the ventral horn, which in all animals play other parts than that of responding to pyramidal impulses, is much more dependent on those pyramidal impulses than it is in the case of the dog.

But this is a digression. The important conclusion to be drawn from the results of the removal of the cortex in the monkey is that the cortex and pyramidal tract are in this animal used for certain special skilled movements, and that in the absence of the cortex and tract those movements cannot be carried out at all, or are carried out in a modified manner only. In the monkey such movements are conspicuous and their absence more or less easily detected; in the dog they are fewer and their absence is more readily overlooked; but fundamentally the two probably agree.

§ **659**. Before we proceed however any further in the discussion, it will be of advantage to turn aside to what is known concerning the Rolandic area in man. As we have already said, theoretical considerations lead us to believe that this area in man is disposed in accordance with the plan of the anthropoid ape as ascertained experimentally, but with the differentiation carried still further; and the few cases of experimental stimulation of the human cortex support this view. Our chief knowledge in this matter is derived from the study of disease; and in this, the advantages of dealing with one of ourselves are largely counterbalanced by the disadvantages due to disease being so often anatomically diffuse and physiologically changeful and progressive.

We said above that during experiments on animals stimulation of any part of the Rolandic area may under abnormal conditions lead to general epileptiform convulsions. Now clinical study has shewn that in man certain kinds of epileptic attacks are of similar cortical origin. In these cases it has been observed that the attack begins in a particular movement, by contractions of particular muscles, or of the muscles of a particular region of the body, of the hand, foot, toe, thumb, &c., and then spreads in a definite order or 'march' over the muscles of other regions until the whole body is involved. When in an experiment on an animal epileptiform convulsions supervene, they similarly start from the region of the body, the cortical area corresponding to which is beneath the electrodes at the time, and similarly spread by a definite 'march' over the whole body. Hence in the human epileptiform attacks of which we are speaking, it has been inferred that the immediate exciting cause of the attack is to be sought in events taking place in that part of the cortex which serves as the area for the movement which ushers in the attack. Further inquiry has not only confirmed this view, but has also shewn that the topography of the cortical areas in man, as thus determined, very closely follows that of the monkey.

Other diseases of the cortex have been marked, among other symptoms, by loss or impairment of particular movements. In many such cases, the cortical lesion has been of such an extent as to involve a number of special areas at the same time, and so to lead to loss or impairment of movement over relatively considerable regions of the body, such as the whole of one arm. Still cases of quite limited mischief do occur, and in many instances it has been possible to diagnose from the failure or impairment of particular movements that a particular area of the cortex was affected by disease. So also in cases where for surgical reasons it has become necessary to remove limited portions of the cortex, the operation has been followed by loss of voluntary power as regards particular movements. And in general the teaching of these cases of disease confirms the deductions from the monkey, and gives us at least some general idea of the topography of the human Rolandic region. Figs. 139 and 140 shew in broad diagrammatic manner the position and relative extent of the areas for the leg, arm and face in man, as far as has yet been ascertained. To assist the reader we give at the same time diagrams, Figs. 137, 138, illustrating the nomenclature of the surface of the human brain.

One area is of special and instructive interest. Speech is an eminently 'skilled' movement. We have seen that in the monkey the area for the mouth and tongue lies at the ventral end of the central fissure or fissure of Rolando, ventral to the arm area, and that the extreme ventral and front part of the Rolandic area just above the fissure of Sylvius supplies an area which we marked as that of phonation (Fig. 134). In the monkey the area of phonation is determined by experimental stimulation; in man, in a similar position, on the third or lowest frontal convolution, sometimes called Broca's convolution, ventral to and in front of, and probably overlapping backwards the area which in Fig. 139 is marked 'face' and which includes the mouth and tongue, clinical study has disclosed the existence of an area which may be spoken of as the area of 'speech.' Lesions of the cortex in this area cause a loss of or interference with speech, the condition being known as *aphasia;* to this we shall presently return. In Fig. 139 this area is shewn in an approximate manner.

The movements of speech are essentially bilateral movements. In the dog and monkey various bilateral movements may be excited by stimulation of the appropriate area in either hemisphere; and analogy would lead us to suppose that in man, the movements of speech would be connected with the speech area in both one and the other hemisphere. The results of lesions however shew that it is in most cases especially the left hemisphere which is connected with speech; it is a lesion in the third frontal convolution of the left hemisphere, often associated with other lesions of the same hemisphere leading to paralysis of the right side of the body and face, which causes aphasia, it being only in exceptional cases that the condition results from a lesion of the corresponding area of cortex in the right hemisphere.

§ 660. We may now return to the discussion of the question, what is the part played by a cortical area, in carrying out the movements with which the area is associated?

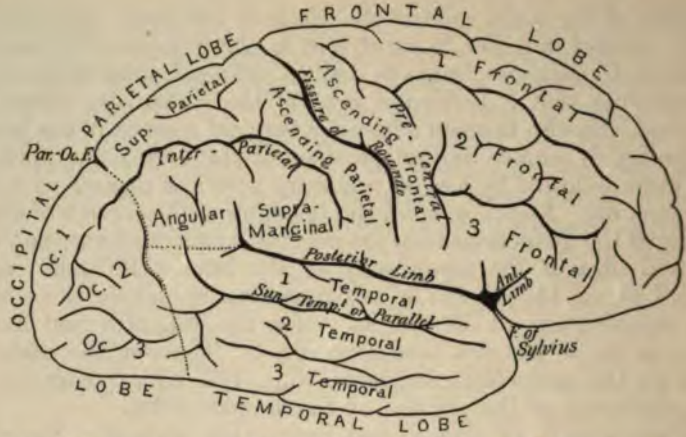

FIG. 137. DIAGRAM OF THE GYRI (CONVOLUTIONS) SULCI, (FISSURES) ON THE LATERAL SURFACE OF THE RIGHT HEMISPHERE OF MAN. (Gowers.)

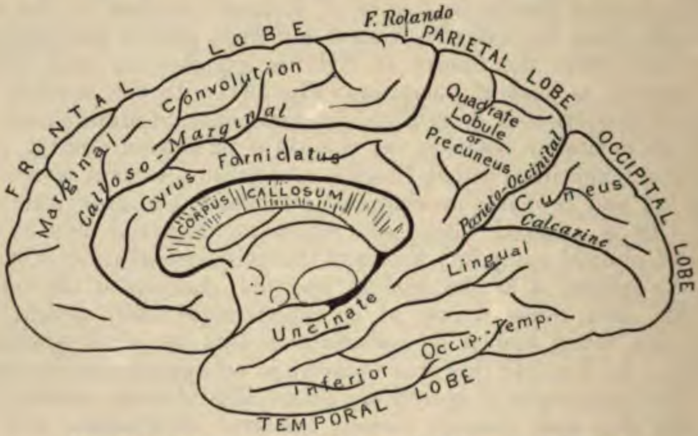

FIG. 138. THE SAME ON THE MESIAL SURFACE. (Gowers.)

In both figures the sulci are indicated by italic and the convolutions by roman type.

The following list of some synonyms may perhaps be of use in connection with these figures and those of the brain of the monkey, Figs. 134, 135.

Gyri, or Convolutions. Precentral or anterior central = ascending frontal. Postcentral or posterior central = ascending parietal. Superior temporal = inframarginal = first temporal. Triangular lobule = cuneus. Central lobe = Island of Reil. Paracentral lobule = the mesial face of the fold connecting the pre- and post-central gyri with a small piece of the most posterior part of the superior frontal. Cingulum = the part of the gyrus fornicatus which adjoins the Corpus callosum. Gyrus Hippocampi = uncinate gyrus, though the latter name is sometimes restricted to the front part of the hippocampal gyrus; the two may be considered as a continuation of the gyrus fornicatus, and the three together, forming a series, have been called "the great limbic lobe."

Sulci or Fissures. Central = Rolandic, or of Rolando. Perpendicular = parieto-occipital. Parietal = intraparietal or sometimes interparietal.

Temporo-sphenoidal lobe = temporal lobe.

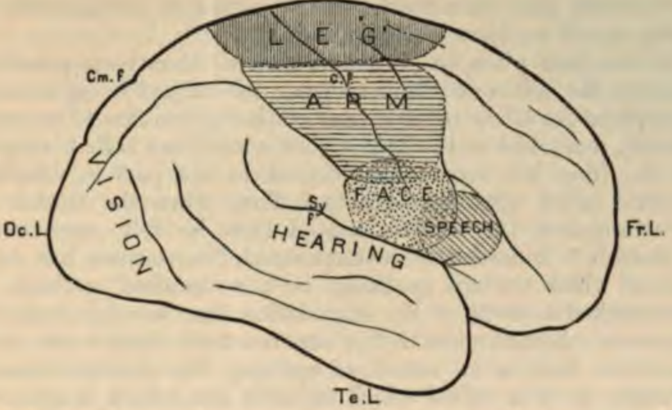

FIG. 139. THE LATERAL SURFACE OF THE RIGHT CEREBRAL HEMISPHERE OF MAN IN OUTLINE, TO ILLUSTRATE THE CORTICAL AREAS. Reduced from nature.

The position of the areas of the cortex concerned with movements of the face, arm, and leg, and with the senses of sight and hearing are approximately shewn. The position of the area connected with speech (Broca's centre) is also shewn for the sake of comparison of it with the position of the other areas; the representation of speech in the cortex cerebri lies however in the *left* hemisphere chiefly.

Oc. L. Occipital lobe; *Fr. L.* Frontal lobe; *Te. L.* Temporal lobe; *Sy. f.* the fissure of Sylvius; *C. f.* the central fissure (Rolandic); *Cm. f.* indicates the position of the posterior end of the calloso-marginal fissure.

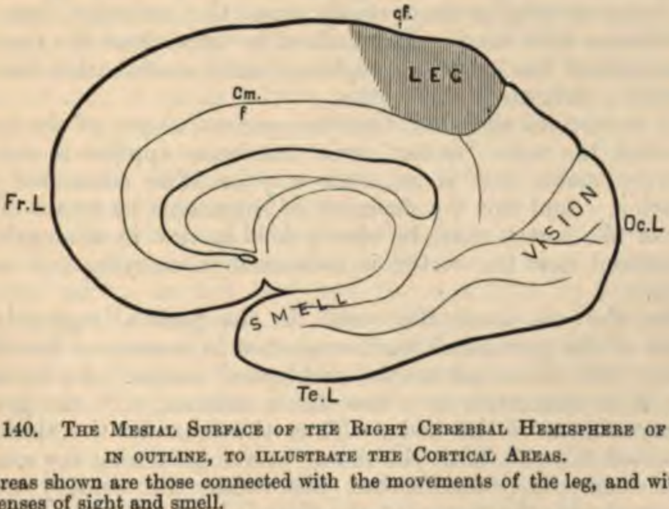

FIG. 140. THE MESIAL SURFACE OF THE RIGHT CEREBRAL HEMISPHERE OF MAN IN OUTLINE, TO ILLUSTRATE THE CORTICAL AREAS.

The areas shown are those connected with the movements of the leg, and with the senses of sight and smell.

Fr. L. the frontal pole of the hemisphere; *Oc. L.* the occipital pole, *Te. L.* the temporal pole. *Cm. f.* the calloso-marginal fissure separating the marginal gyrus above from the gyrus fornicatus below. *Cf.* marks the situation of the central fissure, the fissure itself not being apparent on the mesial aspect of the hemisphere. The corpus callosum and the anterior commissure are seen in cross section.

We must here turn to the consideration of certain facts concerning which we have hitherto been silent.

In the first place, in the cases where it has been possible to stimulate the cortex in a human being, the subject being conscious, the application of the electric current has given rise to sensations variously described as to their nature, sometimes called 'tingling' and the like, but uniformly referred to the part in which the stimulus called forth movements. Thus when the thumb area was stimulated, the subject stated that he felt sensations in his thumb. Indeed the development of sensations has, in the cases of which we are speaking been as marked, perhaps even more marked a result of the stimulation than the development of movement. Accordant with this experimental result is the clinical experience that in an attack of epilepsy, the peculiar sensation or 'aura' as it is called which initiates the attack is referred to the part of the body, the cortical area corresponding to which serves as the starting point of the 'march' of the convulsions. Thus the patient feels a peculiar sensation in his hand or arm just preceding the convulsive movements of the hand or arm by which the attack begins and from which it spreads over the rest of the body.

In the second place when in an animal a portion of the so-called motor area of the cortex has been removed, the loss or impairment of movement has been accompanied by a no less marked loss or impairment of sensation, the recovery from which has been invariably more tardy than the recovery from the interference with movement. Indeed in cases where the recovery of movement has seemed complete, careful examination has still detected a deficiency of sensation.

It is obvious therefore that the parietal region of the cortex to which the term 'motor' area has been applied is not exclusively motor but is in some way or other connected with sensation. And this development of sensations by means of this part of the cortex must be clearly held in view in attempting to understand how the cortex is concerned in carrying out movements.

On the one hand the cortex in the parietal region is, by means of the pyramidal tract, connected in a more or less direct manner with the motor cranial and spinal nerves. At the same time it is connected, in a less direct manner, with the general sensory nerves of the body. Thus the area for the thumb is connected, not only with the motor nerves governing the muscles which move the thumb, but also with the sensory nerves connected with the tissues of the thumb, both those belonging to skin and others. Here, as elsewhere, while the motor limb of the whole nervous mechanism is a simple one, the only relay between the cells in the cortex, and the motor fibres of the spinal roots, being the synapses between the fibres of the pyramidal tract and the cells in the nuclei of the cranial nerves or in the ventral horn of the spinal cord, the sensory limb consists of a series of relays, in the spinal cord, in the bulb and elsewhere. So important is this sensory moiety of the cortical mechanism that it seems to determine the size of the cortical area connected with a particular part of the body. We have already called attention to what appears to be the disproportionate size of the area for the thumb, or the fingers when compared with that of the trunk; but the disproportion vanishes when we measure the value of the thumb, not by its share in the total surface or the total weight of the body, but by the number and complexity of the sensory impulses which pass from it up to the brain. Conversely the movements of the viscera, of which normally we are unconscious, are not represented at all, or in a very exceptional way, in the cortex.

We have already (§ 643) dwelt on the importance of afferent impulses in the development of various movements. Of voluntary movements afferent impulses seem to be, as it were, the very essence. This is shewn by the following important experiments. If in a monkey all the sensory roots belonging to a part, say to the arm, be divided, the result is a loss of voluntary power, which, as regards the extremity of the limb, the hand and digits is complete, but is progressively less marked in the upper parts, in the wrist, elbow and shoulder. No regeneration of the divided roots taking place, the loss in the hand, thumb and fingers at least is permanent; no voluntary power over these parts returns however long the animal may be kept alive. Further, it is the distinctly voluntary movements which are affected. Under the influence of emotions and the like movements may be observed in a limb which, so far as volition is concerned, is useless. We may add that the sensory nerves, whose intact condition thus seems essential to the development of an act of volition, appear to be especially those of the skin as distinguished from those belonging to the muscles, tendons and other parts.

Now, if in an animal which has thus by section of the sensory roots been deprived of voluntary power over, say, its arm, the cerebral cortex be laid bare and the arm area be stimulated, all the usual movements, all the ordinary rough imitations of voluntary movements may be obtained as completely and as readily as, perhaps even more readily than, in an intact animal. This shews, in the case of a normal voluntary movement, how small a part of the whole act is borne by the events taking place in the pyramidal tract, and to what a small extent a movement evoked by stimulation of the cortex corresponds to a really voluntary movement. The fact that the specific movements may be called forth by stimulation, not of the cortex only, but also of the fibres of the tract along their course, for instance in the internal capsule and the electrical phenomena described in § 657, leave little room for doubt but that in the normal function of the pyramidal tract the fibres carry centrifugal impulses from the cortex to the cells whose axons form the fibres of motor nerves. Quite apart from the general question whether an axon whose course lies entirely within the central nervous system (and the fibres of the pyramidal tract are such, being the axons of cells in the parietal region of the cortex) may, when stimulated at a part distant from its perikaryon, transmit impulses centripetally towards the perikaryon as well as centrifugally towards its endings, and, quite apart also from the other general question, whether an axon may not under certain circumstances transmit impulses or influences from its endings centripetally along its whole course, we may probably safely conclude that in carrying out a voluntary movement, the part played by the fibres of the pyramidal tract is simply that of transmitting centrifugally impulses originating in the Rolandic cortex. The experimental results described above shew that those impulses cannot be naturally originated as an act of volition in the cells whose axons supply the pyramidal tract, unless those cells are subject at the time to sensory impulses or influences proceeding from the part which is the seat of the movement. In the voluntary act of adducting the thumb the impulses which, travelling from cells in the 'thumb area' of the cortex along the pyramidal tract, call forth the appropriate contractions of the muscles of the thumb do not arise if those cells are cut off from sensory impulses or influences proceeding from the skin and other tissues of the thumb. It is not as some writers, to judge by their expressions, seem to think, that the 'will,' arising in some way or other out of or in connection with events in the cortex, stimulates the cells in the cortex, whose axons form fibres of the pyramidal tract, to send impulses along the fibres, quite irrespective of what is going on in the rest of the nervous system. On the contrary, the development of the 'will' is contingent on the integrity of the sensory connection between the cortex and the part of the body on which it is about to act (being of course contingent on other things as well), and we have as much right to say that 'the will resides' in the sensory nerves as to say that it resides in the cortex. The following experiment shews that even the rough generation of motor impulses in the Rolandic cortex through artificial stimulation may be influenced by appropriate sensory impulses. If in an animal (dog) while in a particular stage of the influence of morphia a subminimal stimulus be found, that is, a current of such intensity that applied to a cortical area it will produce no movement, but if increased ever so slightly will give a feeble contraction of the appropriate muscles, it may be observed that a slight stimulus, such as gently stroking the skin over the muscles in question, will render the previous subminimal stimulus effective and so call forth a movement. Thus if the area experimented on be that connected with the lifting of the forepaw, and the subminimal stimulus be applied to the area at intervals, after several applications followed by no movements, a gentle stroke or two over the skin of the paw will lead to the paw being lifted the next time the stimulus is applied to the area. A similar result, but less sure and striking, may follow upon the stimulation of parts of the body other than the part corresponding to the area stimulated. Then, again, it has been observed that in certain other stages of the influence of morphia, the cortex and the rest of the nervous system are in such a condition that the application of even a momentary stimulus to an area leads not to a simple movement but to a long-continued tonic contraction of the appropriate muscles. Under these circumstances, a gentle stimulus, such as stroking the skin, or blowing on the face, applied immediately after the application of the electric stimulus to the area, suddenly cuts short the contraction, and brings the muscles at once to rest and normal flaccidity.

§ **661**. We may in this connection profitably consider very briefly one or two points concerning the voluntary movements of speech in man, the evidence touching the connection of which with an area on the third frontal convolution appears so very clear. Speech is eminently a 'skilled' movement; it involves the most delicate coordination of several muscular contractions, and we may certainly say of it that it has to be 'learnt.' Now, the whole chain of coordinated events by which the utterance of a sentence, a word, or any vocal sign is accomplished consists of many links, the breaking of any of which will lead to failure of one kind or another in the act. Something may go wrong in the glossal or other muscles, in the nerve endings in those muscles, or in the fibres of the nerves, hypoglossal and others, between the central nervous system and the muscles, or something may go wrong in that part of the central nervous system, the bulb to wit, in which a certain amount of coordination is carried out just previous to the issue of the motor impulses. Damage done to any of these parts of the mechanism may lead to dumbness or to imperfect speech. In the latter case the imperfections have a certain character; if we are at all able to gather the wish of the speaker, we recognize that he is attempting to utter the right words in the right sequence, but that his efforts are frustrated by imperfect coordination or imperfect muscular action; his speech is 'thick,' the syllables are blurred and the like. Disease of the bulb at times leads to imperfect speech of this kind in which the imperfection may be recognized as due to the lack of proper coordination of motor impulses. The affection of speech, known as 'aphasia,' which is caused by lesions of the cortex is of a different character, and the forms of imperfect speech caused by bulbar disease have justly been distinguished from true aphasia by the use of other terms. Cases of complete aphasia in which all power of speech is lost, do little more than help us to ascertain the topographical position in the cortex of the 'speech' area, but cases of partial aphasia are especially instructive. The striking feature of partial aphasia is the failure to say certain words or syllables, and the tendency to substitute some wrong word or syllable for the right one. The words or syllables which are uttered are rightly pronounced without defect of articulation; and in many cases, though the right word cannot be produced as a direct effort of the will, it may be uttered under the influence of an emotion, or indeed sometimes as the result of some psychical processes more complex than those involved in the mere volitional effort to say the word. An instructive case is recorded of a man suffering from slight aphasia, who after several failures to say the word 'no' by itself, at last said, "I can't say no, sir."

Using the word aphasia in its wide sense of imperfections of speech of cortical origin, we find that there are many different kinds, and some of them have been distinguished by special names. Without attempting to go into any details we may say that the study of such cases (which has the advantage over experiments on animals of an appeal to consciousness) illustrates in a striking manner the theme on which we are dwelling, namely, the large share taken by sensory impulses in the development of a voluntary movement. This is indeed shewn by speech of all kind, perfect as well as imperfect; our speech for instance is directly dependent on our hearing, and he who is born deaf is also mute. But the study of the several cases of aphasia has shewn how many and varied are the sensory factors in the whole complex act of speech. We may recognize what we may perhaps call the more distinctly motor side of the whole business the mechanism of which lies in the third frontal convolution, but the due working of this mechanism is contingent on sensory influences reaching it from distant parts of the cortex. Thus, for instance, cases are sometimes met with in which the patient cannot repeat aloud a word which is spoken to him, though we have evidence that he hears very well, and though he can speak the word when it is shewn to him in type or in writing, or when he is led to wish to utter the word for some reason other than that he has heard it. In such cases the general motor mechanism for speech is intact, as is also the general sensory mechanism for hearing, but the something which brings the auditory sensations conveyed by the latter into relation with the former is wanting, and in consequence the efficiency of the whole speech mechanism is impaired. This is sometimes spoken of as 'auditory aphasia.' Cases of an analogous visual aphasia also occur, and thus in a general way a 'sensory' aphasia has been distinguished from a 'motor' aphasia. Thus (quite apart from its closer connection with the sensory impulses which proceed from the larynx itself, and which are more comparable with the cutaneous sensory impulses so essential as we have seen to the carrying out of a voluntary movement of a limb or part of a limb) the due efficiency of the mechanism of speech is dependent on the due access of sensory impulses from very various parts of the cortex.

Writing is a skilled act, to a certain degree comparable with speech; and a condition of 'agraphia' analogous to aphasia is met with in which the patient cannot write properly; he writes the wrong word or merely makes a scrawl. This condition is similarly due to failure of not the distinctly motor but of the sensory factors.

What is thus shewn in aphasia and the like may also be traced in all our voluntary movements. For instance, in all voluntary movements which affect the position of the body and in which the maintenance of equilibrium is concerned the due activity of the Rolandic cortex is dependent not only on its own integrity, not only on the proper upward sweep of sensory impulses from various cutaneous and other afferent nerves, but also in a special way on impulses reaching it from the vestibular nerve. When a gymnast is executing skilled and carefully learnt voluntary movements in which a multitude of skeletal muscles are simultaneously or successively employed, we may presume, from what we have already learnt, that his Rolandic cortex is in high efficiency, that all the ingoing impulses along sensory nerves and all the outgoing impulses along the pyramidal tract are most carefully adjusted, and that all necessary coordination, be it in the cortex itself or in other parts of the brain, or in the spinal cord at the exit of the ventral roots, is properly effected. But all this is of no avail if some accident should injure his semicircular canal; in the absence of the due vestibular impulses his 'will' would be unable to bring about the discharge of the centrifugal impulses from the cortical pyramidal cells in the proper way.

The predominant importance of sensory elements in the carrying out of voluntary movements by means of the Rolandic area of the cortex is further illustrated by a study of the movements which result from stimulation of regions of the cortex other than the parietal, namely, of the occipital and temporal regions. The movements which may be called forth by stimulation of the occipital region are those of the eyes, and the particular occipital area whose stimulation leads to movements of the eyes is one which, as we shall presently see, is especially concerned in the full development of visual sensations. Here we have a direct connection between sensations, visual sensations proceeding from the retina, and movements of the eyeballs; and there appears to be an anatomical path for such a connection, namely, fibres leading directly from the occipital cortex to the nuclei of the nerves governing the ocular muscles, a path quite distinct from the path afforded by fibres of the pyramidal tract connecting the portion of the Rolandic area concerned in movements of the eyes, with the same ocular nuclei. Thus the important movements of the eyes are presided over by two cortical centres, one in the Rolandic area, the other in the occipital region. An essential condition of the due activity of both centres is the advent from the eyes of sensory impulses. In the case of the occipital area these are the specific visual sensations proceeding from the retina; in the case of the 'eye area' in the Rolandic region they proceed from the muscles and other tissues of the eyeballs. The two mechanisms are distinct, though probably in some way associated together. The movements elicited by stimulating the occipital cortex are not brought about by any indirect effect on the Rolandic area; they continue to appear as usual after removal of the eye area in that region. The connection between the more general sensory sensations derived from the eyeball and the movements of the eyeballs is probably of a simpler character than that between the specific visual sensations and the same movements; hence the results of artificial stimulation are, as we have said, more certain in the former case than in the latter.

Much in the same way as the movements of the eyes thus arising from stimulation of the occipital cortex seem to be connected with visual sensations, so analogous movements of the ear which often result from stimulation of the temporo-sphenoidal cortex seem to be connected with auditory sensations; as we shall see, this region of the cortex seems to be especially concerned in the development of auditory sensations.

Before leaving this subject of the intervention of sensory impulses in voluntary movements, though we shall shortly deal with the development of sensations, we may profitably insert here a warning that that intervention is a complex matter, especially when viewed on the sensory side. The fact that removal of the Rolandic area interferes with sensations and that cutting off sensory impulses entails loss of voluntary movement must not lead us to conclude that the motor effects of stimulating the cortex are caused by the stimulation giving rise to sensations or that in carrying out a voluntary movement we necessarily are directly conscious of, and appreciate as distinct sensations, the sensory impulses which intervene in the act. Cases are recorded of complete hemianæsthesia, that is of loss of sensation over one side of the body, in which full power of voluntary movements, even of skilled and delicate movements, was retained. In such cases the mischief entailing the loss of sensation appears to have been limited to certain higher parts of the brain. And the absence of sensations thus caused marks a different physiological condition from that in which sensations are lost by the blocking of sensory impulses at almost their origin as by the section of the afferent roots. This would seem to point to the conclusion that though sensory impulses are in some way connected with the Rolandic area, the full development of conscious sensations is independent of the proper working of that cortical area. But, as we said, we do not discuss here the nature of sensations, and only mention the above fact in order to prevent any misconception arising from the importance which we have attached to the intervention of sensory impulses in development of voluntary movements.

§ **662**. The histological study of the cortex led us to the conclusion that its dominant feature was a multiplicity of functions by means of which impulses of diverse nature and coming from different sources might meet and play upon each other. This is in complete concordance with the considerations on which we have just been dwelling; we may regard an outgoing manifestation of activity, such as an impulse leading to movement, as the resultant of the impulses confluent at the cortex. The results of artificial stimulation of the parietal region of the cortex have given undue prominence to the motor (pyramidal tract) elements, and this has been further emphasized by the use of the term 'motor' region. But even from what has been already said, it is evident that the sensory elements are at least as important as the motor; we may perhaps place the sensory elements (including their psychical developments) in the first line, and regard the pyramidal tract mechanism as something superadded to and consequent upon the extension and perfection of sensory processes. In this connection it is worthy of note that the afferent fibres passing up to the cortex in the Rolandic area acquire their medulla and presumably become functionally active before the efferent pyramidal fibres proceeding from the same area.

We have seen that a dog from which the Rolandic region of the cortex has been removed can, upon recovery after the operation, carry out voluntary movements so well that it is difficult to detect any deficiency in this respect. Let us take a simpler case, one in which injury to the cortex is avoided, that of a dog in which both pyramids in the bulb have been divided and in which both the pyramidal tracts below the section have degenerated. Such a dog after recovery from the operation, though no regeneration of the pyramidal tract takes place, is able apparently to execute all the ordinary voluntary movements of which a dog is capable. Obviously in such a case the will has access by other paths than the pyramidal tract to the spinal mechanisms connected with the ventral roots of the spinal roots. Yet we can hardly doubt that while the pyramidal tract was intact, the animal made use of it; and we may further infer that the movements of a dog without the pyramidal tracts are different from those of a dog in which these are intact, though we cannot state exactly what the differences are.

When the pyramidal tract is abolished by removal of the Rolandic cortex, the initial loss of voluntary movement is accompanied by loss of sensation; and as we have seen the recovery from the latter is less complete than that from the former. Indeed even with our imperfect means of analysing the sensations of animals, we have evidence tending to shew that sensations never become again exactly what they were before; and we may probably infer that removal of the cortex does entail some permanent loss of sensations, not perhaps of common crude sensations, if we may be allowed the use of such a phrase, but of finer, more or less elaborated sensations. If now we allow ourselves to assume, and there are reasons for our doing so, that the movements which we may call skilled, that is learnt by experience and trial, demand for their due carrying out the cooperation not merely of crude sensations but of the more elaborated ones of which we are speaking, we can appreciate the value of a direct motor path, such as that afforded by the pyramidal tract, between the cortex, which acts so to speak as the nodal point of these elaborated sensations and the motor mechanisms of the cranial or spinal nerves.

In other words, we may roughly distinguish two kinds of voluntary movements, each with its appropriate mechanism. In the first place there are the simpler earlier voluntary movements, whose development demands merely simple sensations, and in carrying out which parts of the brain other than the cortex are very largely concerned. In the second place there are the more complex, finer, skilled movements, for whose development, more elaborated, more psychical sensations, if we may use the phrase, are necessary; these are essentially carried out by the cortex and make use of the pyramidal tract. In carrying out the former the skeletal muscles in all parts of the body may be indifferently used; the instruments of the latter are more particularly those parts of the body, such as the hand with its digits, the sensations from which are most elaborated, and these are as we have seen, especially represented in the cortex.

In animals below the dog skilled acquired movements of the second class are scanty or absent, as is also the pyramidal tract; and as we descend the scale the cerebral cortex becomes, as we have seen, less and less important for the carrying out of the simpler movements of which alone the lower animal is capable.

As we ascend from the dog through the monkey to man the skilled voluntary movements, those which have to be learnt, take up a greater and greater share of the total life, and the pyramidal tract increasing in size comes into greater and greater use. So much so that we may regard it as probable that in man the ordinary mechanism for voluntary movements is that of the pyramidal tract. We may also perhaps add that the more primeval mechanism of voluntary movements, that which obtains in the fish and the frog, and in which the parts of the brain lying behind the cerebral hemisphere play so important a part, has in man fallen in desuetude, and when the pyramidal mechanism fails cannot be trusted to do even its simpler work. And even if this be considered as not as yet distinctly proved, there still remains the conclusion that man's 'will' is, from a physiological point of view, very different from that of the lower animals, much more different than was once thought.

§ **663**. The preceding discussion will enable us to be very brief concerning a question which has from time to time been much discussed, and which has acquired perhaps factitious importance, viz. the question as to how volitional impulses leading to voluntary movements travel along the spinal cord.

There was a time, and that not very long ago, when the results of experimental interference with the spinal cord, such as hemisection of it, in animals seem to point to the conclusion that volitional impulses, crossing over in the region of the bulb travelled down the cord, keeping exclusively to the side to which they had crossed, while sensory impulses entering the cord crossed gradually but speedily over to the opposite side and travelled up to the brain on that opposite side. And such a conclusion was very largely accepted. We shall deal with sensory impulses later on, and confining ourselves now to volitional impulses, we must in considering these bear in mind three important conclusions to which we have been led in the preceding discussions. In the first, the central nervous system, including the spinal cord, differs so much in different animals, and especially in man as compared with other mammals, that we cannot safely deduce from the results of experiments on one kind of animal conclusions concerning another kind; and this applies especially to man. In the second place, we must, if the conclusions to which we have been led by the discussions contained in the preceding sections are just, distinguish between those voluntary movements in which the efferent impulses are carried by the fibres of the pyramidal tract and those which are not. In the third place, we cannot wholly and sharply dissociate volitional and sensory processes; as we have seen, the development of a voluntary movement is contingent on the due procedure of sensory impulses no less than on the integrity of the purely motor part of the volitional mechanism.

Keeping these cautions in view we may consider first the case of the dog. In this animal the particular voluntary movements carried out by means of the relatively small pyramidal tract probably form, as we have seen, a relatively small part of the whole number of its voluntary movements; in a dog which has lost the whole of both its spinal pyramidal tracts by section of the pyramids in the bulb, there seems very little wanting as regards voluntary movement, in spite of the fact that the section of the bulbar pyramids, which contain other fibres than those of the pyramidal tract proper, must have injured nervous mechanisms other than that of the pyramidal tract itself.

Concerning the path of volitional impulses in the dog in the voluntary movements which we may presume to be carried out by means of the pyramidal tract, the only conclusion we can come to is that the impulses follow the anatomical path. That is to say, all or nearly all the volitional impulses cross over at the decussation of the pyramids to the lateral region of the opposite side of the cord (for the direct ventral pyramidal tract is, as we have seen, absent or all but absent in the dog) and continue on that side until they reach the appropriate cells in the ventral horn, and so issue as motor impulses along the ventral roots.

Concerning the path of the larger number of volitional impulses, in carrying which the pyramidal tract takes no part, or so little a part that they seem to be equally well developed in its absence, our knowledge being based chiefly on the results of experiments is far from being satisfactory. It has been found that a section of a lateral half of the cord, a lateral hemisection, or a section limited to the lateral column of one side, has for one of its principal effects loss of voluntary movement on the same side in the parts supplied by motor nerves leaving the cord below the level of the section. We say 'one of its principal effects' because, besides the concomitant interference with sensations concerning which we shall speak presently, the loss of voluntary movement is not absolutely confined to the same side; there is some loss of power on the crossed side, at least in a large number of cases. We must not lay stress on this crossed paralysis because it may be one of the 'shock' effects of the mere operation, not a pure 'deficiency' phenomenon, and indeed appears soon to pass away. Further, in the experience of many experimenters the loss of voluntary power on the operated side also diminishes after a while, and the animal if kept alive and in good health long enough appears to regain almost full voluntary power over the affected parts. In such cases, as in other operations on the central nervous system, there is no regeneration of nervous tissue; the two surfaces of the section unite by connective, not nervous tissue, and the tracts which as the result of the section degenerate downwards or upwards are permanently lost. Hence even if we admit that a voluntary movement of the kind which we are discussing is chiefly carried out by means of impulses passing along the lateral half of the cord, and apparently along the lateral column right down to the motor mechanisms immediately connected with the motor nerves, we must also admit that the 'will' under changed circumstances can find other channels for gaining access to the same mechanisms.

It has been further observed that if in the dog a hemisection be made at one level, for instance in the lower thoracic region of the cord, and then, after waiting until the voluntary power over the hind limb of that side has returned, a second hemisection, this time on the other side, be made at a higher level, this second operation is followed by results similar to those of the first; there is loss of voluntary power on the side operated on, with some loss of power on the crossed side, and as in the first case this loss of power not only on the same but also on the crossed side may eventually disappear. This shews among other things that the recovery after the first operation was not due to the remaining pyramidal tract doing the work of both. Further, the hemisection may be repeated a third time, the third hemisection being on the same side as the first, with at least very considerable return of power over both limbs. That is to say, under such abnormal circumstances voluntary impulses may, so to speak, thread their way in a zigzag manner from side to side along the mutilated cord until they reach the appropriate spinal motor mechanisms.

Such experiments however do not teach us what is the normal path of volitional impulses in an intact animal. Still they do teach us a not unimportant lesson, namely, that the passage of volitional impulses within the nervous system is determined, not only by anatomical, but also by what we may call physiological conditions, a lesson already taught, as regards other impulses, in a very marked way by the phenomena of strychnia poisoning. (Cf. § 586.) A limit to the possible turnings and twistings of a nervous impulse through the maze of the spinal cord is undoubtedly fixed by anatomical structure. An impulse can only pass along a cell or some part of a nerve cell, an axon or a collateral or a dendrite, it cannot wander over the neuroglia, and if it has to change its path, to shift from one track to another, it must find some junction, some synapsis to enable it to get on to another line. But even our present knowledge has opened up for us an almost unlimited number of junctions; and in this respect the short 'ground' fibres of the cord play probably an important part. The orderly tangle of the grey matter of the cord presents a multitude of possible paths, yet all the paths are marked out. We can best explain such vicarious actions as those of which we are speaking, and there are many other such, by supposing that the lines of resistance, determined by physiological conditions, are such that, under normal conditions, the impulse always takes a particular path, but that under abnormal conditions, and among these we may put the blocking of the normal path by section of it, the impulse may wander into other unusual paths.

We may add that this view may be applied as a correction of or caution concerning the conclusion at which we arrived in respect to voluntary movements after loss of the pyramidal tract. We are not justified in inferring that a movement is not carried out by means of the pyramidal tract because it may be carried out in the absence of the tract.

§ **664**. When we reflect on the great prominence of the pyramidal tract in the spinal cord of man as compared with that of the dog, we may justly infer not only that the pyramidal tract is under normal circumstances more exclusively the channel of volitional impulses in man than in such lower animals, but also, bearing in mind the discussion in a previous chapter, § 591, concerning the activities of the spinal cord of man, that the potential alternatives presented by the spinal cord of the dog are greatly reduced in that of man. And such clinical histories of disease or accidental injury in man as we possess support this conclusion. Lesions confined to one half of the cord, or even lesions confined to the lateral column of one half, appear to lead to loss of voluntary power on the same side, and the same side only, in the parts below the level of the lesion; and the same symptoms have been observed to accompany disease limited apparently to the pyramidal tract of one side. Moreover, though cases of recovery of power have been recorded, we have not such satisfactory evidence as in animals of the volitional impulses ultimately making their way along an alternative route.

When we say that the loss of voluntary power is seen on the side of the lesion only, we should add that this statement appears to apply chiefly to the thoracic and lower parts of the cord. We have seen that in man, in the upper regions of the cord, the pyramidal tract is only partly crossed; a variable but not inconsiderable number of the pyramidal fibres do not cross at the decussation of pyramids, but running straight down as the direct pyramidal tract effect their crossing lower down in the cervical and upper thoracic regions. Hence we should infer that a hemisection of, or a lesion confined to one side of the cervical cord, would affect the voluntary movements of the crossed side as well as of the same side, though not to the same extent. But we have no exact information as to this point. And indeed the purpose of the direct tract is not clear; there is no adequate evidence for the view which has been held that these direct fibres are destined for the upper limbs and upper part of the body; since they are the last to cross we should *à priori* be inclined to suppose that they were distributed to lower rather than higher parts.

With respect to the monkey we may say that in regard to the matter which we are discussing, it is intermediate between man and the dog, though much nearer to the former. The passage of volitional impulses along the cord is in the main that marked out by the pyramidal tracts, but the use of vicarious channels, though more distinct than in man, is far more rare than in the dog.

§ **665**. We may now briefly summarise what we know concerning voluntary movements. And it will be convenient to trace the events in order backwards.

Certain muscles are thrown into a contraction which even in the briefest movements is probably of the nature of a tetanus. In almost every movement more than one muscle as defined by the anatomists is engaged, and in many movements a part of several muscles is employed, and not the whole of each. It is perhaps partly owing to the latter fact that a muscle which has become tired in one kind of movement, may shew little or no fatigue when employed for another movement, though we must bear in mind that in a voluntary movement fatigue is much more of nervous than of muscular origin.

Besides the active muscles, if we may so call them, which directly carry out the movement, the metabolism of which supplies the energy given out as work done, other muscles, some of which are antagonistic to the active muscles and some of which may be spoken of as adjuvant, enter into the whole act. In flexion for instance of the forearm on the arm it is not the flexor muscles only but the extensors also which are engaged. According to the immediately preceding position and use of the arm, and according to the kind and amount of flexion which is to be carried out, the extensors will be either relaxed, that is to say inhibited, or thrown into a certain amount of contraction. And in some of the more complicated voluntary movements the part played by adjuvant muscles is considerable. Hence in a voluntary movement the will has to gain access not only to the active muscles, but also to the antagonistic and adjuvant muscles; and every voluntary movement, even one of the simplest kind, is a more or less complex act.

The impulses which lead to the contraction of the active muscles reach the muscles along the fibres of the ventral roots (we may for the sake of simplicity take spinal nerves alone, neglecting the peculiar cranial nerves), and such evidence as we possess goes to shew that the impulses governing the antagonistic and adjuvant muscles travel by the ventral roots also; the question whether the inhibition of the antagonistic muscles when it takes place, is carried out by inhibitory impulses passing as such along the fibres, or simply by central inhibition of previously existing motor impulses need not be considered now. These ventral roots are bundles of axons of cells of the grey matter of the cord, and in each hypothetical segment of the cord we may recognize the existence of an area of grey matter which, though we cannot define its limits, we may, led by the analogy of the cranial nerves, call the nucleus of the nerve belonging to the segment; and we may further recognize in such a nucleus what we may call its efferent and its afferent side.

Every voluntary movement, even the simplest, is as we have repeatedly insisted a coordinated movement, and in its coordination afferent impulses play an important part. The study of reflex actions, § 589, has led us to suppose that each spinal segment presents a nervous mechanism in which a certain amount of coordination is already present, in which efferent impulses are adjusted to afferent impulses. But the results obtained by stimulating separate ventral nerve roots shew that, in the case of most muscles at all events, the especially active muscles of the limbs for instance, each muscle is supplied by fibres coming from more than one nerve root, that is to say, the spinal nucleus, or at least the spinal motor mechanism for any one muscle, extends over two or three segments. Hence *à fortiori* in a voluntary movement, involving as this does in most cases more than one muscle, the spinal mechanism engaged in the act spreads over at least two or three segments, thus allowing of increased coordination. In that coordination the impulses serving as the foundation of muscular sense play an important part, but other afferent impulses, such as those from the adjoining skin, also have their share in the matter; and it is worthy of notice that not only is the skin overlying a muscle served, broadly speaking, by nerve roots of the same segment as the muscle itself, afferent in one case, efferent in the other, but in the parts of the body where coordination is especially complex, in the fingers for instance, not only is each muscle supplied from more than one segment, but also each piece of skin is supplied in the same way by the dorsal roots of more than one nerve.

In the case of the frog it is clear that in reflex movements a large amount of coordination is carried out by these various spinal mechanisms; and as we have urged, we may safely infer that in the voluntary movements of the frog, the will makes use of this already existing coordination, whatever be the exact path by which in this animal the will gains access to the spinal mechanisms. In the dog we may conclude that in voluntary movements the spinal mechanisms, with their coordinating functions, are also set in action, in this case by impulses passing straight from the cortex to the mechanisms of the pyramidal tract, though as we have seen, in the absence of the pyramidal tract, the will can work upon the mechanisms by changes travelling through other parts of the cerebrospinal axis. And in the monkey and man, subject to the doubts already expressed as to the potentialities of the human spinal cord, we may probably also infer that in each voluntary movement some, perhaps we may say much, of the coordination is carried out by the spinal mechanism set into action through impulses along the pyramidal tract. We may probably further infer that a careful adjustment obtains between the beginnings of the pyramidal tract in the cortex and its endings in the cord, so that the topography of 'areas' or 'foci' in the cortex above is an image or projection of the spinal mechanisms below.

But valuing the coordination carried out by the purely spinal mechanism at its highest, this in the genesis of a voluntary movement is insignificant compared with the coordination which takes place in the cortex. Here is tied the knot, the cords of which come from many parts. We have seen that the cortical area from which proceed the pyramidal fibres conveying the impulses which move as an act of the will, any part, such as the thumb, is also an area whither travel the sensory impulses coming from the skin and other tissues of that part; and it is here that by means of the latter the former are coordinated in order to produce movements which no spinal or other mechanism can carry out by itself. Further, in the carrying out of at least many voluntary movements, other sensory impulses are or may be concerned, visual impulses, auditory impulses, the vestibular impulses which enter so deeply into movements affecting the position of the body, and still others. These, reaching the cortical area whence the pyramidal impulses issue, along lines provided by the intricate network of the nervous fibres and fibrils, determine the character of the pyramidal outflow. In every voluntary movement many parts of the brain, indeed of the whole nervous system, other than the particular area, or nodal point which serves as the starting-point of the pyramidal fibres, play their part, and in even a relatively simple movement a large part of the brain is in action.

In an ordinary voluntary movement an intelligent consciousness is an essential element. But many skilled movements initiated and repeated by help of an intelligent conscious volition may, when the nervous machinery for carrying them out has acquired a certain facility (and in all the higher processes of the brain we must recognize that, in nervous material at all events, action determines structure, meaning by structure molecular arrangement and disposition), be carried out under appropriate circumstances with so little intervention of distinct consciousness that the movements are then often spoken of as involuntary. All the arguments which go to shew that the distinctly conscious voluntary skilled movement is carried out by help of the appropriate cortical area, go to shew that the cortical area must play its part in these involuntary skilled movements also. So that, as indeed we have already hinted (§ 661), distinct consciousness is not a necessary adjunct to the activity of a cortical area. And it is worthy of notice that some of these, in their origin, purely voluntary skilled movements, which by long-continued training have become almost as purely involuntary, are hampered rather than assisted by being "thought about."

The word 'training' suggests the reflection that the physiological interpretation of becoming easy by practice is that new paths are made, or the material of old paths made more mobile by effort and use. We have already urged more than once that the grey matter of the spinal cord is a network, in which the passage of impulses is determined by physiological no less than by anatomical conditions, and the same considerations may with still greater force be applied to the brain. We must suppose that training promotes the growth and molecular mobility of the Rolandic area and of all its connections. There are doubtless limits to the changes that can be effected, but within these limits the will, blundering at first in the maze of the nervous network, gradually establishes easy paths; though even to the end it blunders, in trying to carry out one movement it often accomplishes another.

Lastly, without attempting to enter into psychological questions, we may at least say that the birthplace of what we call the 'will,' is not conterminous with the Rolandic area; the will arises from a complex series of events, some of which take place in other regions of the cortex, and probably in other parts of the brain as well. With these parts the Rolandic area has ties concerned not in the carrying out of volition, but in the generation of the will. So that, looking round on all sides, it is obvious, as we have said, that the Rolandic area is a mere link in a complex chain. It is moreover a link of such a kind, that while the changes which the breaking of it makes in the daily life of a lowly animal, such as the dog, in whom the experience of the individual adds relatively little to the nervous and psychical storehouse transmitted from his ancestors, can hardly be appreciated by a bystander, those which the breaking of it makes in the daily life of a man, whose brain at any moment is not only a machine fitted for present and future work but a closely packed record of his past life, are obvious not only to the individual himself, but to his fellows.

SEC. 8. ON THE DEVELOPMENT WITHIN THE CENTRAL NERVOUS SYSTEM OF VISUAL AND OF SOME OTHER SENSATIONS.

Visual Sensations.

§ **666**. In the chain of events through which some influence brought to bear on the periphery of a sensory nerve gives rise to a sensation, we are able, with more or less success, to distinguish between those events which are determined by the changes at the periphery and those which are the expression of changes induced in the central nervous system. Thus when certain rays of light proceeding from an object and falling upon the eye give rise to visual perception of the object, two sets of events happen; the rays of light, by help of the mechanisms of the eye, partly dioptric, partly nervous, give rise to certain changes in the fibres of the optic nerve, which we may call visual impulses; and these visual impulses reaching the brain along the optic nerve give rise to visual sensations and so to visual perception of the object. We shall later on, under the heading of "the senses," deal chiefly with the peripheral events, and have now to consider some points connected with the central events, to learn what we know concerning how the various sensory impulses travelling along the several kinds of sensory nerves behave within the central nervous system. In doing so we shall have from time to time to refer to peripheral events, but only occasionally, and never in any great detail. It will be convenient to begin with the special sense of sight, and we must first briefly call attention to a few points which we shall have to study in fuller detail hereafter.

The eye is so constructed that images of external objects are brought to a focus on the retina, the stimulation of which by light starts the visual impulses along the fibres of the optic nerve; and the distinctness with which, by means of the visual sensations arising out of these visual impulses, we perceive external objects is dependent on the sharpness of the retinal images. The eye is further so constructed that, in any position of the eye, the rays of light proceeding from a portion only of the external world fall upon the retina; or in other words in any one position of the eye

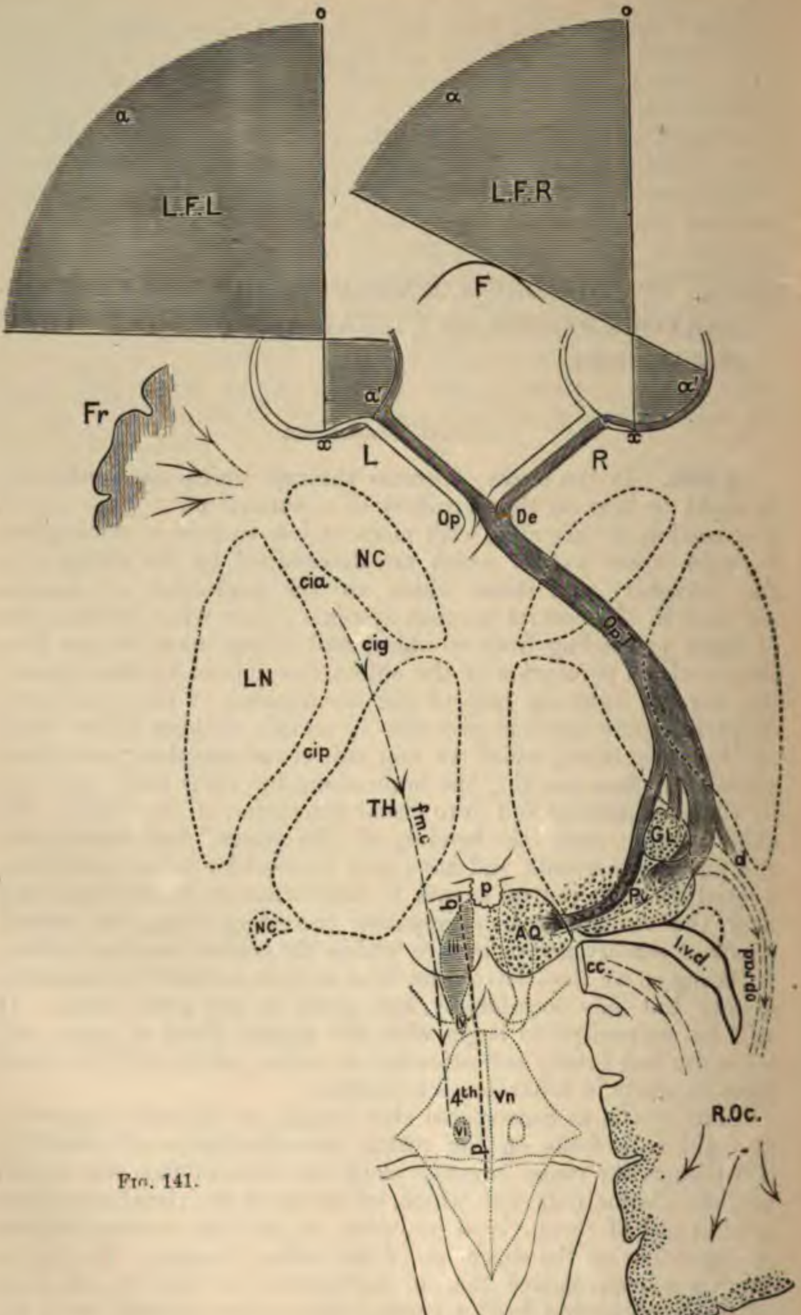
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Fig. 141.

FIG. 141. DIAGRAM TO ILLUSTRATE THE NERVOUS APPARATUS OF VISION IN MAN.

L. the left eye, *R.* the right eye, *o.x.* the optic axis. *F.* the outline of the face between the eyes, *Op.T.* the right optic tract (shaded) supplying, through *Op. De.* the optic decussation, the temporal side of the retina of the right eye and the nasal side of the retina of the left eye. *L. F. L.* and *L. F. R.* the left visual fields of the left and right eye respectively; the two fields and the parts of the two retinas whose excitation produces vision over the fields are shaded, the object *a* in the field of the right side giving rise to an image at *a′*, and *a* on the left side an image at *a′*.

The right optic tract is represented as ending in *GL.* the lateral corpus geniculatum, in *Pv.* the pulvinar, and in *AQ.* the anterior corpus quadrigeminum, all three stippled; *op. rad.* the optic radiation from these bodies to *R. Oc.* the right occipital lobe, whose stippled cortex indicates the "visual area." *d.* the 'direct' tract to the cortex. *c. c.* corpus callosum, cut across at the splenium, *l. v. d.* descending horn of the lateral ventricle.

The left side has been utilized to indicate at *F.* shaded with lines, the cortical motor area for the eyes; *fm. c.* indicates the path from it to III. IV. VI. the nuclei of the third, fourth and sixth nerves. *p. b.* the posterior longitudinal bundle, shewn as a broken line. *NC.* the nucleus caudatus, *LN.* the nucleus lenticularis and *TH.* optic thalamus shewn in outline, *Cia.* the front limb, *Cig.* the knee, and *Cip.* the hind limb of the internal capsule. The outlines of the fourth ventricle 4th *Vn.* and of the posterior corpora quadrigemina are shewn by dotted lines, that of the bulb is shewn by a fine line. *p.* the pineal gland.

only a portion of the external world is visible at the same time. The portion so seen is spoken of as the *visual field* for that position.

The image thrown on the retina is an inverted one, so that the top of an actual object is represented by the lower, and the bottom by the upper part of the retinal image; similarly the actual left-hand side of the retinal image corresponds to the right-hand side of the actual object, and the right-hand side to the left-hand side. Hence the right-hand half of the visual field corresponds to the left-hand side of the retina, and the left-hand half to the right-hand side.

The eye can be moved in various directions, and since in the visual field the portion of external nature which can be seen at the same time differs with each different position, a large range of vision is thus secured; and this can be further increased by movements of the head. Moreover we normally make use of two eyes, our normal vision is binocular; and the visual field of the right eye differs from that of the left eye. There is one striking difference which must always be borne in mind. A section carried through the eye in a vertical and front-to-back plane, through what we shall learn to call the optic axis (Fig. 141, *ox*) (the exact details of the plane may be left for the present), will divide the retina into two lateral halves, and in each retina one half will be on the nasal side next to the nose, and the other half will be on the malar or temporal side, next to the cheek or temple. It must be remembered that the nasal halves and temporal halves of the two retinas do not occupy corresponding positions in space. The temporal half of the left retina is on the left side of its own eye, whereas the temporal half of the right retina is not of the left but on the right side of its eye; and so with the nasal halves. Now, in the right eye, the right-hand side of the visual field corresponds to the nasal half of the retina, and the left-hand side of the visual field to the temporal half of the retina, whereas in the left eye the right-hand side of the visual field corresponds to the temporal half of the retina, and the left-hand side to the nasal half. This is shewn in Fig. 141, where the left-hand visual field and the retinal area concerned are shewn shaded in each eye.

When we look at an object with the two eyes, though two retinal images are produced, one in one eye and one in the other, we perceive one object only, not two. This is the essential fact of binocular vision; when certain parts of each retina are stimulated at the same time we are conscious of one sensation only, not two; and the parts of the two retinas which, stimulated at the same time, give rise to one sensation are spoken of as "corresponding parts." From the structure and relations of the two eyes it follows that the temporal side of the right and the nasal side of the left eye are such corresponding parts, while the nasal side of the right eye corresponds to the temporal side of the left eye. But the whole of each retina is not employed in binocular vision. Owing to the position of the two eyes in relation to the nose, it comes about that an object held very much on one side, to the left-hand side for instance, while it is capable of producing an image on the extreme nasal side of the left eye, and can be seen therefore by that eye, cannot produce an image on the temporal side of the right eye; the nose blocks the way. It is therefore not seen by the right eye, and the vision of it is monocular, by the left eye only. In Fig. 141 it may be seen that the left visual field of the left eye (*L.F.L*) extends more to the left, and is larger than the left visual field of the right eye, *L.F.R*, and that the right retinal area, corresponding to the left visual field, extends farther along the nasal side of the left side (α'), than it does along the temporal side of the right eye (α'), the difference being due to the presence of the nose (*F*). And similar conditions obtain with regard to the extreme right-hand side of the visual field.

§ **667**. After these preliminary statements, we may now turn to consider some anatomical facts concerning the ending of the optic nerve in the brain.

The optic nerve of each eye consists of nerve fibres coming from all parts of the retina of that eye; but the two optic nerves meet, ventral to the floor of the third ventricle, cross each other at the *optic chiasma* (Fig. 141, *op. De*), and are thence continued on under the name not of optic nerves but of *optic tracts* (*Op.T.*). The decussation of fibres which takes place in the chiasma has peculiar characters. At their decussation (we are speaking now of man) the fibres in the optic nerve belonging to the temporal half of the eye in which the nerve ends pass into one optic tract, namely, the optic tract of the same side, while the fibres belonging to the nasal half pass into another optic tract, namely, the optic tract of the opposite side. Thus the fibres of the temporal half of the right eye and of the nasal half of the left eye pass into the right optic tract, and the fibres of the nasal half of the right eye and of the temporal half of the left eye pass into the left optic tract. Compare Fig. **141**, in which the fibres forming the right optic tract are shaded while those forming the left optic tract are left unshaded. Now, the nasal half of one retina and the temporal half of the other retina are 'corresponding' parts. Hence, while each optic tract contains fibres belonging to half of each eye, the two halves thus represented in each tract are corresponding halves.

The amount and character of the decussation taking place in the optic chiasma differs in different animal types, the differences having relation to the amount of binocular vision, which in turn depends on the position of the eyes in the head, that is, on the prominence of the face between the eyes. In the fish for instance, with laterally placed eyes, no binocular vision at all is possible, and the decussation is complete; the whole optic nerve of each eye crosses over to the other optic tract. Between this and the arrangement in man just described, various stages obtain in various animals.

The chiasma also contains at its hinder part fibres which have no connection with the optic nerves or the eyes, but are simply commissural tracts passing from one side of the brain, namely, from the median corpus geniculatum (§ 630) along one optic tract, through the chiasma to the other optic tract, and so to the median corpus geniculatum of the other side of the brain. These fibres are spoken of as the *inferior* or posterior (optic) *commissure* or arcuate commissure, or Gudden's commissure. It was once thought that in a similar way fibres passed from one retina along one optic nerve, through the front part of the chiasma to the other optic nerve, and so to the other retina forming an anterior (optic) commissure; but this seems to be an error.

§ **668**. The optic vesicle is, as we have seen, budded off from the fore-brain or forerunner of the third ventricle, and the optic chiasma is attached to and forms part of the floor or ventral wall of that ventricle. In a view of the basal or ventral surface of the brain the diverging optic tracts are seen to separate the anterior perforated space and lamina cinerea in front from the posterior perforated space, tuber cinereum with the infundibulum, and corpora albicantia behind, all these being parts of the floor of the third ventricle. From the grey matter in this floor fibres, forming what is sometimes spoken of as Meynert's commissure, belonging neither to the optic nerves nor to the inferior commissure, join the optic tracts, eventually leaving them to pass to the pes. Hence the whole of the optic tract is by no means derived from the optic nerve, the fibres just mentioned and the inferior commissure form parts of the optic tract not connected with the retina.

Each optic tract crosses obliquely, being in crossing firmly attached to, the ventral surface of the crus cerebri of the same side, Fig. 112 *C*, and is soon lost to view, being covered up by the temporo-sphenoidal lobe of the hemisphere. When this is removed the tract is seen to sweep dorsally round the crus, towards the dorsal aspect and, as we have already (§ 630) said, to become connected on the farther side of the crus with the two *corpora geniculata*, lateral and median. We may say at once that the median corpus geniculatum has no connection with that part of the tract which is derived from the optic nerve, and is not concerned in vision, but is connected with that part of the tract, sometimes called the median part, which goes to form the inferior commissure. We may confine our attention to that part of the tract which consists exclusively of fibres coming from the retinas of the two eyes, for it is this part, and this part only, which is concerned in vision.

§ 669. This ends in three ways, as shewn diagrammatically in Fig. 141. In the first place, a large part of the tract ends in the lateral corpus geniculatum (*GL*). In the second place, a large number of fibres passing the corpus geniculatum on its ventral and lateral surfaces spread out into the pulvinar (*PV*). In the third place others, in less but considerable number, taking a more median direction, reach the anterior corpus quadrigeminum (*AQ*).

We must not enter into the details of the minute structure of these three bodies but must content ourselves with saying that each consists of alternating layers of white and grey matter, the latter containing different kinds of cells, most of which are remarkably rich in dendrites. The fibres of the optic nerve, as we shall see when we come to deal with the eye and vision, are for the most part axons of cells in the retina, axons carrying impulses, visual impulses centripetally to the brain. When we trace the fibres through the optic tract to the anterior corpus quadrigeminum, we find them entering into and forming a large part of the superficial layer or zone of white matter. Thence they plunge into the underlying grey matter and there end in extensive arborisations by which they form synapses with certain of the cells of the grey matter. In many cases at least the fibres while running in the superficial white matter branch or give off collaterals, which also may end in similar arborisations. A similar arrangement obtains in the lateral corpus geniculatum and the pulvinar. The optic fibres, carrying visual impulses, end in one or other of the three bodies by synapses with constituent cells of those bodies.

The optic nerve contains, besides afferent fibres carrying centripetal impulses just spoken of, a much smaller number of fibres which are the axons of cells not of the retina but of certain cells in one or other of the three bodies with which we are dealing, chiefly, if not exclusively, the anterior corpus quadrigeminum.

These fibres therefore do not begin but end in the retina, and may be presumed to carry impulses centrifugally from the brain to the retina.

The intimate connection between the retina and the three bodies in question thus disclosed by histological investigation is further shewn by the following experimental facts. We know that when a nerve fibre is cut away from its nerve cell it degenerates; but the division, and the loss of the peripheral degenerating portion, has comparatively little effect on the nerve cell; when a spinal nerve, for instance, is divided below the spinal ganglion, though the nerve below the section degenerates, the ganglion and the piece of nerve in connection with it remain very much as before, though special examination may disclose some changes in the features of the nerve cells. We have it, however, in our power to bring about changes of a deeper and wider character, a cessation of growth amounting to atrophy, by operative interference with nervous structures before they are fully developed. Thus in an adult animal, a section of an optic nerve or removal of the eye leads to degeneration in the optic nerve and optic tract; the optic fibres have their trophic centre in certain cells of the retina, of which we shall speak in treating of vision, and cut away from that centre they degenerate; by this means the nature of the optic decussation in animals, and indeed in man, has been ascertained. But if the eyes be removed (removal of both eyes being desirable on account of the characters of the optic decussation) in a new-born animal, not only do both the optic nerves and the greater part of both optic tracts cease to be further developed and degenerate, but the bodies mentioned above, the two lateral corpora geniculata, the pulvinar on each side, and the two anterior corpora quadrigemina do not fully develope; certain parts of them undergo atrophy. The development of these nervous structures seems therefore to be largely dependent on their functional connection with the eyes by means of the optic tracts and nerves.

The same method confirms the view expressed above that the median corpus geniculatum has no connection with vision. When the eyes of new-born animals are extirpated neither the median corpora geniculata nor the posterior corpora quadrigemina shew any sign of atrophy, and the part of the optic tract which does not degenerate is the inferior commissure connecting the two median corpora geniculata. We may add that in the mole, in which vision is meagre and the optic nerves are slight, the inferior commissure and the median corpora geniculata are well developed. Obviously these parts are associated with functions of the brain other than those of sight. The lateral corpora geniculata, the pulvinar and the anterior corpora quadrigemina, are, we may repeat, alone to be regarded as the chief central parts in which the optic nerves end. We may also repeat that in the higher animals owing to the peculiarity of the optic decussation each optic nerve thus finds its endings in both sides of the brain.

While the optic chiasma is, as we have seen, helping to form the floor of the third ventricle, it gives off fibres to the posterior perforated spot. Some of these have been supposed to pass directly in the wall of the ventricle to the nucleus of the third (oculo-motor) nerve, and to serve as a channel for afferent impulses, causing constriction of the pupil; but to this we shall return in dealing hereafter with the movements of the pupils.

§ **670**. Though the above three bodies are undoubtedly the chief endings of the optic nerve, it has been stated that some fibres of the optic tract, making connections with neither of these three bodies, pass by the crus cerebri straight to certain parts of the cerebral hemisphere (Fig. 141, *d*) supplying a "direct" cerebral tract; but there is increasing evidence that this view is an erroneous one. We may probably with great confidence assert that the connection of the cerebral hemisphere with the optic tract is not a direct one, but an indirect one, through the three bodies in question.

We called attention in § 633 to a set of fibres occupying the hind limb of the internal capsule, connected with the occipital cortex, and known by the name of the 'optic radiations.' The greater part of these fibres may be traced to the lateral corpus geniculatum and to the pulvinar of the thalamus (Fig. 141). Without entering into too much detail we may say that in each of these bodies are certain cells, relatively large and richly provided with dendrites, the axons of which may be traced into the optic radiations and, we have reason to think, end in the occipital cortex by making synapses with the cortical cells. These cells are in connection with the fibres of the optic nerve ending, as we have seen, in the two bodies in question. Probably the connection is not a direct one; probably the optic fibres end in arborisations round the dendrites of cells of Golgi also found in abundance in these bodies, and the short-branched axons of these cells of Golgi form in turn synapses with the cells mentioned above as sending their axons up to the occipital cortex. Be this as it may, the fibres of the optic nerve, by a relay, more or less complex, in the lateral corpus geniculatum and pulvinar, are connected with fibres proceeding through the optic radiations to the occipital cortex.

Mixed with the other fibres of the optic radiations are fibres which may be traced to the anterior corpus quadrigeminum, reaching that body by its anterior brachium (§ 634). But there seems no doubt that a large number at least of these fibres are the axons, not of cells in the corpus quadrigeminum, but of cells in the occipital cortex. They may be assumed to be fibres carrying impulses, not like those of the corpus geniculatum and pulvinar to the cortex, but from the cortex. It has indeed been urged that all these fibres are of this kind, that there exist no fibres which may be presumed to carry impulses from the corpus quadrigeminum to the occipital cortex. This perhaps cannot as yet be considered as definitely proved; on the other hand it has been maintained that the cortex sends through the optic radiations similar fibres to the pulvinar, if not to the corpus geniculatum, fibres carrying impulses from the cortex to the lower bodies; but obviously the connections of the corpus quadrigeminum, as part of the visual nervous mechanism, are different from those of the corpus geniculatum and pulvinar. In fact, the anterior corpus quadrigeminum may be considered as being in part a mechanism, putting the motor nuclei of the 3rd, 4th and 6th cranial nerves (to which it sends fibres) in connection with the retina on the one hand by a long path for afferent impulses, up to the occipital cortex and back again to the corpus quadrigeminum, and on the other hand by a short path direct from the retina to that body.

The intimate connection between the three bodies in question, but especially the lateral corpus geniculatum and pulvinar, and what we may at present speak of as the occipital cortex (we will attempt to define its limits later on) is shewn by the following experimental results. When even in a grown animal (rabbit, cat and dog) the occipital cortex is destroyed, not only the fibres of the optic radiations but also parts of the lateral corpus geniculatum and pulvinar undergo degeneration, and there is some change in the anterior corpus quadrigeminum. The degeneration thus observed is not, we may remark in passing, a degeneration resulting from the severance of axons from their trophic centres, *i.e.* from their cells. So far at least as the majority of the fibres of the optic radiations are concerned the removal of the cortex only entails the removal of the terminals of axons; yet as the result of that removal the cells giving off those axons degenerate. The loss of the terminal prevents the impulses, whatever be their exact nature, which pass up along the axon from the pulvinar &c. to the cortex, from producing their proper effects; and this failure in some way or other affects the nutrition of the whole cell. The degeneration is an indirect degeneration due to interference with function, and probably may be brought about in parts of the central nervous system other than those which we are studying now, though it has not been observed in peripheral nerves. Its occurrence may profitably be taken as a warning of the great complexity of the passage of what we call a nervous impulse along the elements of the central nervous system. We are perhaps too apt to think that when a change in a cell of say the pulvinar, excited by a visual impulse along the optic fibres, produces a change in the occipital cortex, the cell having discharged a wave-like "impulse" along its axon, is heedless of the future fate of the wave so soon as it has left the perikaryon. The facts with which we are dealing suggest that the cell keeps, so to speak, in some way or other in touch with the impulse wave which has left it, and that when a change in the pulvinar cell gives rise to visual sensation, the cell in the pulvinar and the cell or cells in the cortex work together as a whole; the material of each of them and of the whole length of the tie between them, is as it were vibrating at the same time. When the cortical cell is cut off from the pulvinar cell the latter is no longer subject to the same molecular agitations as before; as a consequence its nutrition suffers, and it finally wastes away. Such is the more probable explanation of the degeneration which certainly takes place. It might be urged that the degeneration is an indirect effect of the loss of fibres carrying impulses from the cortex to the lower bodies. But these fibres go chiefly at least to the corpus quadrigeminum, whereas the degeneration is most marked in the other bodies. This however is a digression; the main fact before us is that the occipital cortex has close connections with the three bodies with which we are dealing, especially with the pulvinar and corpus geniculatum. We may add that while the connection of the cerebral cortex with the corpus quadrigeminum (or optic lobe) seems to be a primary one, and is in the lower animals a prominent one, this in the higher animals seems less prominent, owing to the increasing predominance of the connection with the corpus geniculatum and pulvinar.

We have seen that in new-born animals section of the optic nerves or removal of both eyes leads to atrophy of the three bodies under discussion. We have now to add that this, as might be imagined, is accompanied by changes of the nature of atrophy in the occipital cortex, especially in its fibres. We have further to add that while in the adult animal the effect of the removal of the occipital cortex seems to stop at these three bodies, the optic tract and nerve remaining at least as a rule intact, removal of the same cortex in the new-born animal leads also to atrophy of the optic tract and nerve.

Lastly, we may state that the results of operations on animals are corroborated by those of disease in man. Cases are on record in which disease of the occipital cortex has been accompanied by degenerative changes in the pulvinar and corpus geniculatum.

From all the above facts we may conclude that in the act of vision the three bodies with which we are dealing form an important relay on the visual path. Impulses started in the retina travelling as 'visual impulses' along the optic nerve and tract produce certain changes in those bodies, and as the result of those changes, changes of another order, the basis of what we call visual sensations and perceptions are excited in the occipital cortex. In other words, in the complex act of vision two orders of central apparatus are involved; we may speak of two kinds of centres for vision, the primary or lower visual centres supplied by the three bodies in question, and a secondary or higher visual centre supplied by the cortex in the occipital region of the cerebrum. And experimental results as to the effect on visual sensations of interference with the occipital cortex accord with this view.

Before we proceed to discuss those results, one or two preliminary observations may prove of use.

In the first place, as we have previously urged, the interpretation of the results of an experiment in which we have to judge of sensory effects is far more uncertain than when we have to judge of motor effects, that is of course when the experiment is conducted on an animal. We can estimate the motor effect quantitatively, we can measure and record the contraction of the muscle; but in estimating a sensory effect we have to depend on signs, our interpretation of which is based on analogies which may be misleading. We are on safer ground when we can appeal to man himself in the experiments instituted by disease; but the many advantages thus secured are often more than counterbalanced by the diffuse characters or the complex concomitants of the lesion. In dealing with sensory effects we must expect and be content for the present with conclusions less definite and more uncertain even than those gained by the study of motor effects.

In the second place, in dealing with vision, it will be desirable to know the meaning which we are attaching to the words which we employ. By blindness, that is 'complete' or 'total' blindness, we mean that the movements and other actions of the body are in no way at all influenced by the falling of light on the retina. Of partial or incomplete or imperfect vision, using the word vision in its widest sense, there are many varieties; and we may illustrate some of the defects of the visual machinery, regarded as a whole, with its central as well as its peripheral parts, by referring to certain defects of vision due to changes in the eye itself. The eye may fall into such a condition, that the mind can only appreciate, and that to a varying degree, the difference between light and darkness; the mind is aware that the retina (or it may be part of the retina) is being stimulated to a less or greater degree, but cannot perceive that one part of the retina is being stimulated in a different way from another part; a sensation of light is excited, but not a set of visual sensations corresponding to the sets of pencils of luminous rays, which, reflected, or emanating from external objects in a definite order, are falling upon the eye. The eye, again, may fall into another condition, in which such sets of visual sensations are excited, but on account of dioptric imperfections or for other reasons the several sensations are not adequately distinct; the mind is aware through the eye of the existence of 'things,' but cannot adequately recognize the characters of those things; the visual images are blurred and indistinct. And a large number of gradations are possible between the extreme condition in which those objects only which present the strongest contrast with their surroundings are visible, to a condition which only just falls short of normal vision. Imperfections of this kind, of varying degree, may result from failure not in the peripheral apparatus, not in the retina, or optic nerve or other parts of the eye, but in the central apparatus; the retinal image may be sharp, the retina and the optic fibres may be duly responsive, but from something wrong in some part or other of the brain the visual sensations excited by the visual impulses may fail in distinctness, and that in varying degree. Imperfections of vision, whether of central or peripheral origin, in which visual sensations fail in distinctness are generally spoken of under the not wholly unexceptionable name of *amblyopia*.

If one optic nerve be divided, total blindness of one eye will result; but if one optic tract be divided, it follows from what has been said above, that half-blindness in the corresponding halves of both eyes will result. If, for instance, the right optic tract (Fig. 141, *Op. T.*) be divided, the *left* visual fields of both eyes will be blotted out. The same condition will be brought about by failure in the optic tract at its central ending, provided of course the mischief be confined to the ending of the one tract. Such a half-blindness or half-vision is spoken of as *hemianopsia*, or *hemianopia* or *hemiopia*; the words left and right are generally used in reference to the visual field; thus left hemianopsia is the blotting out of both left visual fields, through failure of the right optic tract.

If instead of the whole optic nerve being divided certain bundles only were cut across, partial blindness would be the result, a portion of the visual field would be blotted out; and mischief limited to a few bundles of one optic tract might lead to corresponding blots in the corresponding halves of the visual fields of both eyes.

Further, an affection of half the retina or of a limited area in the retina might occur of such a character as to lead not to complete, but to partial blindness, to a hemi-amblyopia or to a partial amblyopia. The part of the retina so affected might be central, or peripheral, it might be a quadrant, or a patch of any size, form and relative position. And we may further imagine it at least possible that mischief in the brain might be so limited as to produce any of the above partial effects, though the retina, optic nerve, and optic tracts all remained intact.

The above visual imperfections we have illustrated by changes in the peripheral apparatus, but there is a kind of imperfection which we may still call a visual imperfection, though it is of purely central origin. In a normal state of things a visual sensation, excited in the brain, is or may be linked on to a chain of psychical events; we often then speak of it as a visual idea. When we see a dog, the visual sensation, or rather the group of sensations making up the visual perception of the dog, does not exist by itself, apart from all the other events of the brain; it joins and affects them, and among the events which it so affects may be and often are psychical events; the visual perception 'enters into our thoughts' and modifies them. Between the visual impulse as it travels along the optic nerve or tract and its ultimate psychical effect a whole series of events intervene; and we may take it for granted that the chain may be broken or spoilt at any of its links, at the later as well as at the earlier ones. We may therefore consider it possible that the break or damage may occur at the links by which the fully developed visual sensation joins on to psychical operations. We may suppose that an object is seen and yet does not affect the mind at all or affects it in an abnormal way.

These foregoing considerations emphasize the difficulty and uncertainty of interpreting the visual condition of an animal which has been experimented upon. When, for instance, after an operation an animal ceases to be influenced in its previous normal manner by the visual effects of external objects, a most careful psychical analysis is often necessary to enable us to judge whether the newly introduced disregard of this or that object is due to the mere visual sensations being blurred or blunted, or to some failure in the psychical appreciation of the sensations; and in most cases such an analysis is beyond our reach. The greatest caution is needful in drawing conclusions from experiments of this kind, especially from such as appear to have been hastily carried out or hastily observed; and we must be content here to dwell on some of the broader features only of the subject.

§ **671**. Before we speak of the effects of removal of the occipital cortex we may say a few words concerning the effects of stimulating it.

We have already said (§ 661) that electrical excitation of the occipital cortex behind the Rolandic region may produce movements, but that these movements are in character different from those caused by stimulation of the Rolandic region itself. In the monkey stimulation of parts of the occipital region, the occipital lobe and the angular gyrus for instance, may give rise to movements of the eyes, of the eyelids, and of the head, that is of the neck, all the movements so produced being such as are ordinarily connected with vision. It will not be profitable to enter here into the details concerning the exact topography of the excitable parts or of the special characters of the movements so called forth. But it is important to note that these movements are unlike the movements excited by stimulation of the appropriate Rolandic area inasmuch as their occurrence is far less certain, they need a stronger stimulus to bring them out, when evoked they are feeble, being easily antagonized by appropriate stimulation of the Rolandic area, and they have a much longer latent period. They are not due to any indirect stimulation of the Rolandic area, through "association" fibres connecting the spot stimulated with that area, or otherwise, since they persist after its removal. Movements of this kind may also be witnessed in the dog. In both animals they are obviously the result of impulses transmitted in some direct manner from the cortex to some parts below, and as we have just seen, § 670, we now possess direct histological evidence that cells in the occipital cortex send down axons which pass to and end in the anterior corpus quadrigeminum, and through that body are brought into connection with the nuclei of the nerves governing the muscles of the eye and also with other nervous motor mechanisms. In other words, the occipital cortex possesses a system of fibres carrying impulses centrifugally from the cortex to motor nervous mechanisms connected with the eyes, comparable to the pyramidal tract which carries similar impulses to the motor nervous mechanisms of the skeletal muscles in general. Much in the same way that in the Rolandic area the activity of the pyramidal fibres is associated with general sensations of touch and the like, that of those among them which start from the 'eye' area being associated with such general sensations from the tissues of the eyeball, so the activity of these fibres from the occipital cortex is especially associated with visual sensations, and particularly perhaps we may add visual perceptions, started by changes in the retina. In this respect the occipital cortex is as much 'motor' as the parietal cortex. And it is perhaps worthy of note that large pyramidal cells occur in the occipital as in the parietal cortex.

§ **672**. Turning now to the effects of removal of the cortex we may pass lightly over the results which have been obtained in the dog and lower animals; for, in the first place, as we have already so often insisted, the structural arrangements differ widely from those in man, in the amount of decussation of the optic fibres for instance, and in the second place the difficulties of ascertaining what changes in vision have been brought about are exceedingly great. It will suffice to say that in these animals removal of the occipital cortex (we are purposely at present using the general term occipital) does interfere with vision in a way and to an extent not witnessed after the removal of any other part of the cortex. Removal of part or of the whole of the occipital cortex on one side produces imperfect vision or partial blindness, or blindness in one (the opposite) eye, and removal of the occipital cortex on both sides brings about a condition which may provisionally be spoken of as total blindness. The results of removal, in fact, most distinctly corroborate in a broad way the conclusions which may be deduced from the anatomical facts discussed above.

In the monkey, whose central nervous system is so much more like that of man, the decussation of the optic fibres being in particular very similar, the results of experiment in the hands of various observers have not been wholly accordant; but bearing in mind the difficulties of interpretation already referred to, and still using the general term occipital cortex, all the experiments lead to the broad conclusion that this part of the cortex is concerned in vision in a way and to an extent that no other part of the cortex is. The most general result of such experiments is that removal of the occipital cortex on one side leads to crossed hemiopia; the removal of the right cortex causes loss of vision in the two left visual fields; that is to say, the visual impulses passing from the two right halves of the retinas along the right optic tract fail to produce their usual effect so that the animal disregards objects on its left-hand side. Removal of the occipital cortex on both sides produces in the monkey as in the dog apparent total blindness.

In man, the study of diseases of the cortex, while also yielding results not wholly accordant, nevertheless most clearly supports the view that the occipital cortex is specially concerned in vision. Lesions of the occipital cortex on one side are accompanied, according to their extent and severity, by complete crossed hemiopia or hemi-amblyopia, or to defects of vision of some kind or other in the crossed visual fields; that is to say, the impulses passing along one optic tract fail in part or in whole to produce their proper effect.

Thus experiments on animals and clinical observations on man, viewed in the light of the anatomical facts, leave no doubt but that when we 'see,' something of the following takes place. The changes in the retina evoked by the action of light give rise to visual impulses which pass along the optic nerves and optic tracts to the lower visual centres, and these produce changes, the result of which in turn is that impulses or nervous events of some kind or other are transmitted along the optic radiations to the occipital cortex, arrived at which, and not until then, they become transmuted into or in some way develop conscious sensations and perceptions.

This broad result is clear, but beyond this the way to sure and precise conclusions becomes difficult.

In the first place, there is uncertainty as to the exact limits of the area of the cortex in the occipital region thus concerned in vision. In the monkey the majority of observations point to the occipital lobe itself, to the area marked 'vision' in Figs. 134, 135; but other observations, including the earlier ones, seem to shew that the visual cortex, if we may use the word, is that surrounding the angular gyrus (Fig. 133). In man clinical observations lead to the conclusion that the cuneus (Fig. 138) and the parts of the adjoining lobus lingualis bordering on the calcarine fissure are preeminently visual; but there are reasons for including as well the occipital gyri, first, second, and even the third, as being visual, and some observations point to the superior and inferior parietal as being also concerned in the matter. At present it is not possible to define accurately and surely the visual area.

In the second place, the existence of a visual area in the cortex being granted, there is as yet much uncertainty as to whether, in vision as a whole, the different districts of this area play different parts, and if so what is the part played by each separate district; it is obvious that an adequate solution of this problem might clear up the contradictions or want of accordance mentioned above as to the exact parts of the cortex concerned in vision. For instance, it seems reasonable to suppose that each part of the retina is so connected with a particular part of the cortex that the retina may be considered as projected on to the cortex, the right halves, for instance, of the two retinas being projected on to the right cortex, so that the latter bears as it were an image of the former; and many observations support this idea. Thus it has been urged that the cortex dorsal to the calcarine fissure corresponds to the upper, and that ventral to it to the lower half of the retina. Both the anatomical facts and experiments as well as clinical observations seem, as we have seen, to point to the conclusion that half the retina is connected with, is projected as it were on to, the cortex of one side, and one side only. If this be so our vision of the external world consists of two halves carefully pieced together along a vertical seam of which we are never at any time or under any circumstances conscious. But, if this were so, total blindness due exclusively to cortical disease could only occur when the two visual areas in the two hemispheres were both rendered useless, and would naturally be extremely rare, whereas among cases of deficiency of vision of purely cortical origin they are not so uncommon, and cases of total amblyopia, that is of imperfect vision equally marked on both sides of the field of vision, are relatively frequent. Further, it would seem unlikely that the adjustment of the two halves of the field of vision which must be, and indeed is, complete should be left to be carried out simply by means of the callosal commissural fibres ensuring the joint action of the two cerebral hemispheres.

And indeed, though it is true that the one half of the retina may be said, if we do not take into consideration any particular parts of it, to be structurally and functionally united with the cerebral hemisphere of one side, it is not true of a special part of it. We shall in dealing specially with the sense of sight speak of the central part of the retina in man, the part which is called the macula lutea (or yellow spot) with its fovea centralis, as the part of the retina in which vision is most distinct, and which, when in ordinary sight we direct our attention to any object, is used far more than any other part. Now clinical observations point most distinctly to the conclusion that in man this central part is connected with, is projected on to, both cerebral hemispheres; thus when a lesion of the visual cortex of one hemisphere causes what appears to be a complete hemiopia careful examination shews, in many cases at least, that while practically one-half of the field of vision is obliterated the median border of the obliteration passes by the macula lutea, or at least the fovea centralis, so that the whole of this and not a lateral half only of this remains functionally active. Further, it has been suggested, and much may be said in favour of the suggestion, that this central region of the retina is not connected solely with, is not projected as a small piece on to a limited part of the visual cortex, but is, so to speak, diffused over the whole or greater part of the visual area. Such a view opens up many problems and suggests that the complexity of the whole visual process is much greater than would appear from the general description given above, though the uncertainties and discordances to which we have referred may perhaps be taken as pointing in the same direction. In this relation it will be desirable to return to a consideration of the lower visual centres.

§ **673.** As we have said, the evidence is so strong that we may regard it as proved that all the fibres of the optic tract end in one or other of the primary visual bodies. Whatever therefore takes place in the cerebral cortex is the result not only of the visual impulses travelling along the fibres of the optic tract, but also of the events taking place in the primary visual bodies, whereby the visual impulses are modified so that what passes on to the cortex is in some way different from that which reaches the primary bodies along the optic tract. Of these three bodies the lateral corpus geniculatum and pulvinar are in this respect more important than the corpus quadrigeminum (indeed, as we have seen, it may be doubted whether the latter, in the higher animals at least, takes any part in the development of distinctly conscious, psychical sensations), and the corpus geniculatum seems more important than the pulvinar. In man a lesion limited to the pulvinar or to the corpus quadrigeminum may produce no obvious disturbance of vision, whereas a lesion of the corpus geniculatum always does. And indeed there is evidence that this latter body is especially connected with the macula lutea, that is to say, the part of the retina most used in attentive sight. Now we are probably justified in concluding that the events in the cortex are psychical, that the action of the cortex is necessary for the elaboration of precise conscious sensations such as can alone supply the basis of perceptions; but we are not justified in assuming that the whole elaboration takes place in the cortex and in the cortex alone. The close nutritive connection between the cortex and the cells of the corpus geniculatum and pulvinar suggests that the two work together in a special manner, that the cells of the latter cannot work properly unless they are, so to speak, in touch with the cortex; it is because they cannot work properly that they degenerate when cut off from the cortex. Hence it seems a fruitless task to attempt to discuss how far vision can be carried on in the absence of the cortex; for even immediately after the operation, to say nothing of the effects of shock, the primary visual bodies are no longer acting as they were in concert with the intact cortex, and at later periods degeneration progressively robs them of what was at first left to them.

We have, it is true, seen in a previous section that the frog and the bird certainly, and according to some observers also the rabbit, are in the absence of the cerebral hemispheres not totally blind, their movements being guided by retinal impressions; and cases are recorded of the dog being obviously still guided in some measure by retinal impressions after the occipital lobes had been wholly or almost wholly removed. It may be added that though in a bird the removal of a cerebral hemisphere seems to produce complete blindness in the opposite eye, if the other eye be extirpated it becomes obvious that the bird is in some way guided by the eye which before seemed to be perfectly blind. In view however of the facts just mentioned we seem driven to the conclusion that in such cases as the above the influence of light produces its effect by some nervous mechanism different from that by which ordinary psychical vision is carried on. Whether the activity of such an inferior mechanism is accompanied by consciousness or not is a separate question, and one into which we cannot enter here. We will only remark that such an inferior vision, if we may so call it, such a simpler influence of light on movements seems to be chiefly carried out by the anterior corpus quadrigeminum. In dealing specially with vision we shall have to consider the movements of the eyes, including the movements of the pupil in relation to light falling on the retina, and shall discuss the nervous mechanism, including the part played by the corpus quadrigeminum. In the meantime we are at present dealing with conscious visual sensations, and have been led to speak of this inferior mechanism by way of digression.

It is worthy of notice that each of the bundles of fibres connecting the pulvinar and corpus geniculatum with the cortex has a larger cross-section than that of the optic tract itself, that belonging to the corpus geniculatum being the larger of the two. And histological examination would lead us to conclude that each optic fibre entering the corpus geniculatum and pulvinar becomes connected through synapses with, and so is capable of acting upon more than one cell sending up an axon to the cortex. If this be the case, then, whatever 'projection' of the retina and of the visual field obtains in the cortex cannot be of such a kind that each spot or minute area in the retina, impulses from which travel along a single fibre of the optic tract, finds its exact counterpart in the cortex as it might do did those impulses travel onward again to the cortex by a second single fibre. As we have said, there is probably some sort of 'projection'; but this is of such a kind that a primary projection takes place in the primary visual bodies, the pulvinar &c., and a secondary projection from this on to the cortex. And this conclusion seems supported by clinical observation. A limited lesion of the occipital cortex does not, as might be expected from the doctrine of projection as ordinarily expounded, lead to a blotting out of a small bit of the field of vision, but either seems to have no effect at all on vision, or to produce only a diffused weakness or amblyopia. Further, the peculiar relations of the central region of vision may perhaps be explained by the supposition that the optic fibres arising from this part not only proceed to the primary visual bodies of both sides, but within those bodies on each side make wider and larger connections with the cells of those bodies than do the other optic fibres. In other words, distinctness of vision is not the result of narrowed impulses, but a more precise judgment effected by means of ampler material to work upon.

Lastly, the view of the important share taken in the elaboration of a complete visual sensation by these primary bodies seems to point to a way of reconciling the discrepancies referred to above in the attempts to define accurately the visual area of the cortex and to localise its constituent parts. As we have said, the experimental evidence gained from the monkey is conflicting as to the occipital gyri or the angular gyrus being especially connected with vision as a whole. And anatomical evidence points to both being in some way concerned in the matter. But they may be concerned in different ways. For instance clinical study seems to shew that the angular gyrus has especially to do with what has been called 'word-vision,' and its connection with speech. We have seen that there is a kind of aphasia in which the patient cannot understand and so cannot repeat by speech a heard word though he can a printed or written, that is, a seen one. There is another kind of aphasia in which the patient cannot understand and so cannot repeat by speech a seen, though he can a heard word, and this latter kind of aphasia seems to be connected with lesions of the angular gyrus. This is one of many instances of the complexity of psychical vision, a complexity which on general grounds alone we might assume to exist; and the basis of that complexity probably lies in the work of the primary visual bodies. At the same time the initiation of complexity in these lower bodies probably renders possible a greater or less vicarious action of the cortex so far as the broader features of vision are concerned.

Sensations of Smell.

§ 674. The olfactory nerve, which is undoubtedly the nerve of smell, stands like the optic nerve apart from the rest of the cranial nerves; and a few words as to its structure and relations will be necessary.

Lying on the ventral surface of the anterior region of each hemisphere, on each side of the anterior fissure, is seen the olfactory bulb, which is prolonged directly backwards as the olfactory tract, coming apparently to an end where the hind margin of the frontal lobe abuts on the anterior perforated space in the floor of the front part of the third ventricle. The bundles of fibres forming the olfactory nerve proper spring from the bulb, which is their immediate cerebral origin, both bulb and tract being really parts of the cerebrum. Just as the fore-brain buds off on each side the optic vesicle to form the optic nerve, so each cerebral vesicle buds off an olfactory vesicle, the front part of which becomes the rounded bulb and the remainder the rounded trigonal tract or peduncle connecting the bulb with the hemisphere. In man the original cavity of the vesicle is obliterated, being filled up with neuroglial gelatinous substance, but in the lower animals it remains as a linear space, the ventricle of the olfactory tract.

The bulb is a specialized mass of grey matter, forming a sort of cap to the end of the tract, and presents some analogies with the cortex of the hemisphere. Along the middle line lies the core of neuroglial gelatinous substance; but the side of the bulb dorsal to this core, in contact with the hemisphere, is much less developed than the side lying ventral to the core, next to the cribriform plate; and we may confine ourselves to the ventral portion. Next to the neuroglial core lies a layer of longitudinal medullated fibres, with which are mingled some nerve cells. This layer, which forms the beginning of the tract inside the bulb, is thinnest at the rounded front extremity of the bulb and gradually thickens backward. Next to it lies a 'nuclear' layer, composed of small cells, the so-called 'nuclear' cells, arranged to a large extent in longitudinally disposed groups. Fibres from the preceding layer pass between the groups, which are moreover separated by interlacing bundles of fibres. Next to this layer comes a somewhat thick one, which perhaps may be compared to the molecular layer of the cerebellum or to the pyramidal layers of the cerebrum. It is composed of a molecular ground substance, partly neuroglial in nature, traversed by numerous fibrils and fibres, many of the latter being of the fine medullated kind; it also contains, in no large number in man, nerve cells, some of which from their more or less triangular form and extensive dendrites are not unlike the pyramidal cells of the cortex. They have been called *mitral* cells; the larger of them are generally found near the nuclear layer. Next to this molecular layer, or 'gelatinous layer' as it is sometimes called, comes, still working outwards towards the surface, a characteristic layer in which are found the 'olfactory glomeruli'; and outside this is the layer of olfactory fibres. These fibres, which are in reality bundles of fine fibrils, are arranged in a close-set plexus, and from the plexus bundles pass at intervals through the pia mater which invests the bulb and furnishes it with an ample supply of blood; having so passed the fibres acquire sheaths, and form the olfactory nerve proper.

Each fibril of a bundle of the olfactory nerve is, as we shall see when we come to deal with the sense of smell, a prolongation of a special cell in the olfactory or Schneiderian membrane of the nose. These special cells are in reality peripheral nerve cells, and we may regard the fibril as an axon. Tracing the bundles from the olfactory membrane through the pia mater and layer of olfactory fibres we find that a bundle, or more than one, plunges into a glomerulus, within which each fibril branches into a complex nest-like arborisation, each of the terminal twigs of which ends in a minute knob. The mitral cells, as we have said, resemble the pyramidal cells in possessing extensive dendrites. Two or more of the dendrites of each cell spread laterally in the molecular layer, but one, which may be compared perhaps to the apical dendrite of a pyramidal cell, is directed to and enters a glomerulus, in which it terminates in a brush-like arborisation twining in and among the arborisations of the olfactory fibrils. Each glomerulus is in fact a complicated synapsis between the olfactory fibrils and the 'brush' dendrite of a mitral cell. The further exact relations of the olfactory cells to the mitral cells differ in different animals. In animals with an acute sense of smell, macrosmatic animals, the number of mitral cells in proportion to olfactory cells (and therefore fibrils) is very high; neighbouring olfactory cells may form synapses with separate mitral cells, and several mitral cells may send their brush dendrites to one common glomerulus. In other animals on the other hand one mitral cell may supply several glomeruli. The axon of the mitral cell passes through the nuclear layer to the superficial layer of longitudinal fibres, giving off several fine collaterals on its course, and there becomes one of the fibres of the olfactory tract. Thus the olfactory impulses generated in the olfactory membrane of the nose undergo a relay in the olfactory glomeruli by means of a synapsis which is remarkably conspicuous, and pass, presumably in a modified form, along the fibres of the olfactory tract. It may be added that besides the axons of the mitral cells which may be assumed to carry impulses from the olfactory bulb to the brain, the tract contains fibres which are the axons of cells placed in some part or other of the brain, which end by branching in the molecular layer of the bulb, and which, like the somewhat corresponding efferent fibres of the optic nerve, may be assumed to carry impulses from certain parts of the brain to the olfactory bulb.

The central connections of the olfactory tract are too complex to be dealt with here in detail. The sense of smell plays a far less conspicuous part in the life of man than it does in the lives of most of the lower animals; indeed so far as the sense of smell is concerned, man may be regarded as a degenerate animal, and the whole nervous apparatus for smell seems to be in him in a retrograde condition. In most of the lower animals the parts of the brain in connection with the olfactory bulb are much more developed than in him, though the amount of development differs in different animals, being small in those, such as the cetacea, which appear to have little or no smell; and most of our knowledge of the subject is based on the study of animals in whom the sense of smell seems keen. Putting the matter very briefly we may say that the olfactory tract, lying in a groove of the cerebral hemisphere into which it sends fibres from its upper keel-like surface, at the end of the groove divides into a number of parts which are sometimes spoken of as its "roots" and which have very different destinations. One a median one, large and conspicuous in some animals, passes into the anterior commissure (§ 635) and so reaches the other side; it also sends fibres into the front end of the gyrus fornicatus and into the gyrus subcallosus, which latter is in man small and atrophied. Part of the tract ends in the grey matter of the anterior perforated space; but the most important part is the lateral root, which sweeping laterally across the anterior perforated space and the mouth of the fissure of Sylvius, passes to the front end of the hippocampal gyrus, often called the uncinate gyrus.

The fibres of the tract as this starts from the bulb are to a large extent axons of the mitral cells of the bulb, though with these, as we have said, are fibres ending, not beginning in the bulb, coming from elsewhere and apparently carrying impulses to the bulb. Along the tract are small masses of grey matter, collections of nerve cells, in which axons coming from the bulb end by synapses, and from which fresh axons start; these cells in fact serve as relays; while some of the axons of the mitral cells thus end in relays, it is maintained that others pass right along without relays. Hence the tract as it proceeds consists partly of long fibres coming from the bulb, axons of mitral cells, and partly of short fibres beginning in the tract itself. Of the several destinations of the fibres of the tract it must suffice to say here that those passing to the hippocampal gyrus (and these come from the mitral cells either directly or through a relay), end, chiefly at all events, by forming synapses with the cells of the cortex of that gyrus.

§ **675**. The above anatomical facts suggest that the hippocampal gyrus, and perhaps more especially the uncinate end of it, is largely concerned in the development of olfactory sensations; and such evidence as we possess supports that conclusion.

In the first place, the gyrus is largely developed in animals whose sense of smell is keen. In the second place, removal of or operative interference with the gyrus has frequently, though not invariably, led to loss or impairment of smell. In the third place, clinical study seems to shew that in man a lesion involving the cortex of this gyrus, but leaving the olfactory bulb and tract intact, may destroy or greatly impair smell. Strongly pointing in the same direction is the experience that in the cases of cortical epilepsy in which the premonitory aura takes on the form of a peculiar smell, this gyrus has been found to be diseased.

On the whole, then, we may probably conclude that the cortex of the uncinate gyrus is in some way connected with the development of olfactory sensations. But the fact that this gyrus is only one of the several terminations of the olfactory tract warns us that the matter with which we are dealing is a complex one. Some of the fibres of the median root, passing by the anterior commissure are destined for the uncinate gyrus of the other side, and so may simply provide for crossed action, but others, as we have said, go to other parts, for instance to the gyrus fornicatus. It is possible that, after the analogy of the optic tract and its three endings in the lower visual centres, the olfactory tract may develope olfactory sensations in more ways than one.

It is tempting to compare the olfactory with the visual nervous mechanism. We may safely compare the olfactory membrane with the layer of rods and cones of the retina, and the olfactory bulb with the deeper parts of the retina, the mitral cells corresponding to what we shall later on speak of as the ganglionic cells of the retina. But when we attempt to compare the olfactory tract with the optic nerve and tract we meet with a difficulty. In the former are the collections of grey matter whose cells serve as relays for some at least of the fibres of the tract. There are no such relays along the optic tract; the optic fibre when it has left the retina meets with no cell until it has reached the one or other of the lower visual bodies. Are we to consider then these comparatively insignificant groups of cells as the analogues of the corpus geniculatum, quadrigeminum and pulvinar? or is the grey matter of the uncinate gyrus, although it is cortical in nature, the analogue of the lower visual body? If we adopt the latter view we must look elsewhere for the mechanism developing the full psychical olfactory sensations. Now we do find the grey matter of the uncinate gyrus in special connection by means of what elsewhere in the cortex would be called 'association' fibres with that infolded part of the hippocampal gyrus which is called the cornu Ammonis; and these fibres may serve in smell a function corresponding to that of the optic radiations in sight. But the whole of this matter requires further investigation.

Lastly, we may add that indirectly either by the uncinate gyrus and the cornu Ammonis, or by the other terminations of the fibres of the olfactory tract, the olfactory mechanism is brought into connection with other parts of the brain, with portions of the tegmental region for instance, and thence with motor mechanisms. It is probably through these secondary connections that the involuntary and other movements associated with smell are carried out.

Sensations of Taste.

§ **676**. This special sense though so closely associated with smell stands, together with the special sense of hearing, on a different footing from the two preceding special senses, since the nerves concerned belong to the category of ordinary cranial nerves.

We shall see in dealing with the senses that the fifth nerve and the glossopharyngeal nerve have been considered as nerves of taste, but that the matter is one subject to controversy; the gustatory function of the fifth is, for instance, attributed to the peculiar chorda tympani nerve, and other questions have been raised. Whatever view we take, however, the nerves of taste are ordinary cranial nerves, and we have no anatomical guidance as to the fibres of either of the above two nerves making special connections with any part of the cortex. Though sensations of taste enter largely into the life of animals, and indeed of man himself, we have no satisfactory indications which will enable us to connect this special sense with any part of the cortex; the view indeed has been put forward that some part of the cortex in the lower portion of the temporal lobe, not far from the centre for smell, serves as a centre for taste; but the arguments in favour of this view are not, as yet at least, convincing.

Sensations of Hearing.

§ **677**. The cochlear division of the eighth or auditory nerve may be assumed to be a nerve of the special sense of hearing, and of that alone; the vestibular division serves, as we have seen, for other functions than those of hearing, § 642; indeed it is maintained by many that it does not serve at all for hearing. Without prejudging this question, on which we shall have something to say when we are dealing with the senses, we may here confine our attention to the impulses passing along the cochlear nerve and consider only the development of auditory sensations out of these.

We may first turn to the anatomical evidence; this we have attempted to illustrate by a diagrammatic figure, Fig. 142. In § 618 we traced the fibres of the cochlear nerve to the cochlear nucleus consisting of the tuberculum acusticum and accessory nucleus; the fibres end by forming synapses with the cells of these bodies. The axons of the cells thus played upon by the auditory impulses form two afferent strands. One gathered chiefly from the tuberculum acusticum but also from the accessory nucleus, passes dorsal to the restiform body and appearing on the floor of the fourth ventricle is there known by the name *striæ acusticæ*. The other gathered from the accessory nucleus alone passing ventral to the restiform body runs transversely in the depths of the pons as the *corpus trapezoides*. Both these strands pass into or make connections with the lateral fillet (cf. § 634 and Figs. 116, 117, 118), but their course and connections are complicated.

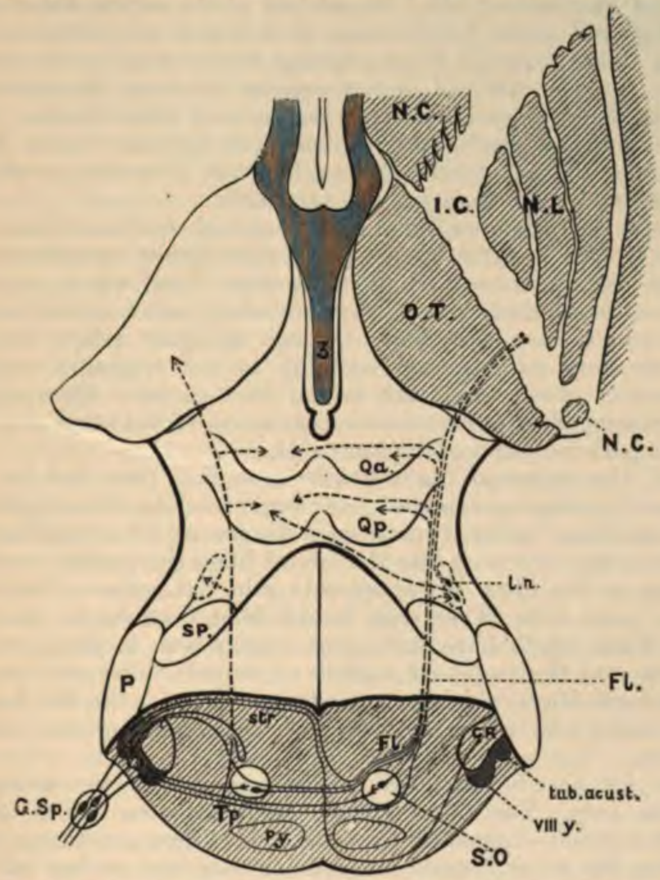

FIG. 142. DIAGRAM TO ILLUSTRATE THE PATHS OF AUDITORY IMPULSES.

The Pons is represented as being cut through vertically and the parts in front as seen from above, the optic thalamus and corpus striatum being however cut through horizontally on the right-hand side.

G. sp. Ganglion spirale. *tub. acust.* tuberculum acusticum. VIII. *y.* accessory nucleus. *Py.* Pyramidal fibres. *C. R.* Restiform body. *S. O.* Superior olive together with the trapezoid nucleus. *Tp.* Trapezoid fibres. *str.* Striæ acusticæ. *F. l.* lateral fillet. *P.* Middle peduncle of cerebellum. *S. P.* superior peduncle. *l. n.* Lateral nucleus. *Q. p.* Posterior and *Q. a.* anterior corpus quadrigeminum. *O. T.* Optic thalamus. *N. C.* Nucleus caudatus. *N. L.* Nucleus lenticularis. *I. C.* Internal capsule. 3. Third ventricle.

In the tegmental region of the bulb and pons is a mass of grey matter called the superior olive (cf. Figs. 114, 115, 116), which has by some authors been divided into parts, and near this in connection with the trapezoid fibres lies another small mass of grey matter called the nucleus of the corpus trapezoides. (In Fig. 142, these for the sake of clearness are shewn as one body.) The trapezoid fibres running transversely in the depths of the pons, in part end in the superior olive and the trapezoid nucleus, forming synapses with the cells of those bodies. The greater number passing the median raphe join the bodies of the other side, and are therefore 'crossed' fibres. But some, a smaller number, end in the bodies of the same side.

From the superior olive and trapezoid nucleus fibres, the axons of cells in those bodies, pass longitudinally upwards in the lateral fillet. Hence this fillet contains fibres, which we may speak of as auditory fibres, impulses along which, after leaving the cochlea have undergone through synapses relays first in the accessory nucleus, and secondly in the trapezoid nucleus or superior olive. And each lateral fillet contains fibres of this kind coming chiefly from the cochlear nerve of the other side but also in part from that of the same side.

All the trapezoid fibres however do not thus end in the trapezoid nucleus or superior olive; some reaching the neighbourhood of those bodies, turn from a transverse to a longitudinal direction and so run up into the lateral fillet, the greater number passing to the fillet of the opposite side, but some to the fillet of the same side. Thus each lateral fillet contains on the one hand fibres which have undergone a relay both in the accessory nucleus and the trapezoid nucleus or superior olive, and on the other hand fibres which have undergone a relay in the former body only; and while most of both kinds are 'crossed' some are not.

So far for the trapezoid fibres supplied by the accessory nucleus only. The fibres of the striæ acusticæ which come chiefly but not exclusively from the tuberculum acusticum, after running for some distance superficially on the surface of the anterior part of the fourth ventricle plunge ventrally into the tegmentum, making for the superior olive. But, so far as our present knowledge goes, they do not join and do not form synapses with the cells of that body; but suddenly changing their course in its neighbourhood and bending upwards as longitudinal fibres pass into the lateral fillet. As is the case with the trapezoid fibres, most of the fibres of the striæ acusticæ crossing the raphe pass to the other side, and are therefore crossed fibres; but some are uncrossed, and join the lateral fillet of the same side.

Hence the impulses which leave the cochlea find a pathway along the lateral fillet, but the pathway is a complex one. As we have seen, § 618, each cochlear fibre as it passes into the brain bifurcates into an ascending and descending branch, the former passing to the accessory nucleus, and the latter, as a rule, to the tuberculum acusticum, which lies rather behind the accessory nucleus in relation to the cochlear root. The meaning of this bifurcation, which is a feature of all or nearly all afferent roots, is not at present clear; but we may perhaps be justified in assuming that the impulses passing along one branch are in some way of a different character from those passing along the other; though they both travel along the same path, namely, the fillet, their behaviour is probably in part different. A large number but not all of the impulses which passing along the ascending branches are carried to the accessory nucleus, and thence ventrally along the trapezoid fibres, undergo a second relay and we may assume suffer a second change in the trapezoid nucleus or superior olive; while none of the impulses passing along the descending branches to the tuberculum acusticum, and thence dorsally along the striæ acusticæ, undergo a second relay but travel along the lateral fillet after having suffered such changes only as befall them in the cells of the tuberculum.

If we assume, as we seem to have reason for doing, that the cells of the accessory nucleus and tuberculum correspond to the lower layers of the complex retina (the structures in the cochlea itself and in the ganglion spirale corresponding to the upper layers of the retina), the striæ acusticæ and trapezoid fibres may be considered as corresponding to the optic nerves and tract; and it is worthy of notice that in both optic and auditory paths the decussation of fibres is large.

One point in connection with the striæ acusticæ remains to be mentioned. Some of the fibres having crossed the raphe do not make for the superior olive but sinking rapidly to the ventral surface of the pons sweep round the ventral surface of the pyramidal fibres and make their way to the inferior cerebellar peduncle and so to the cerebellum. If the impulses along these fibres, and we are assuming that all the impulses along the cochlear nerve are auditory, affect consciousness by being brought to bear on the cerebral hemispheres, they must produce their effects whatever they may be in a very roundabout manner.

To return to the lateral fillet. As this runs forward in the tegmental region of the front part of the pons, it passes by the side of a small collection of grey matter known as the "lateral fillet nucleus." Collaterals from the fibres of the fillet pass into this nucleus and form synapses with its cells; and from its cells proceed axons which, joining the fillet, pass upward as constituent fibres of it. We have no right to assume that all the fibres of the lateral fillet are continuations direct or indirect (by synapsis) of the trapezoid fibres and striæ acusticæ and therefore engaged in carrying auditory impulses. And our present knowledge is insufficient to decide whether the particular fibres which thus make connections with the lateral fillet nucleus are auditory fibres or fibres of another kind, and therefore whether that nucleus is to be considered as a part of the auditory nervous mechanism or no. But on the whole the presumption is in favour of such a view.

The lateral fillet thus reinforced by fibres from its nucleus is continued forward, and may be said to end in the corpora quadrigemina, both posterior and anterior, but chiefly the former, some of the fibres in each case ending on the same side but others crossing. It may be added that the fibres which cross here are the fibres which have already crossed in the pons before they joined the fillet; the fibres from the cochlear nucleus which pass up in the lateral fillet of the same side appear to join the corpora quadrigemina of the same side only.

But though the corpora quadrigemina may thus in a general way be considered as the ending of the lateral fillet, there is trustworthy evidence that some of the fibres pass still further forward and taking at first the direction of the optic radiations, with which they may be considered analogous, reach and end in the cortex of the temporo-sphenoidal lobe, and more especially to that of the first or superior temporal convolution.

The results, on which the above description is based, have been obtained partly by direct observation with the silver or methylene blue method, partly by the method of degeneration and atrophy, and though there are still some differences of opinion, have been very generally accepted. Put in a broad way, the conclusions which may be deduced from them concerning the development of auditory sensations are somewhat as follows. Taking the nervous impulses which leave the cochlear nucleus (the tuberculum acusticum and accessory nucleus) as being of the same order of events as the visual impulses passing along the optic nerves and tracts, these acquire their full development as conscious psychical auditory sensations when they reach and produce changes in the cortex of the temporal convolutions, especially of the superior. And for the most part such impulses are thus developed in the hemisphere of the opposite side. On their way they undergo an initial development in lower auditory centres, the superior olive, trapezoid body, and possibly the lateral fillet nucleus, corresponding to the corpus geniculatum and pulvinar in the case of visual sensations; but while the direct cerebral tract in the case of visual sensations, conveying impulses from the optic tract to the cerebral cortex without the intervention of the 'lower visual mechanisms' seems disproved, there appears to be more reason to believe in such a direct cerebral tract in the case of auditory sensations.

On their way the auditory impulses, not as yet distinct psychical sensations, however much they may have been developed and changed since they left the cochlear nucleus, are brought into connection with the nervous mechanisms of the lower brain, especially with those concerned in carrying out movements. The auditory work of the superior olive and the lateral fillet nucleus is probably not limited to the mere shaping of auditory impulses; it probably includes the bringing those impulses into touch with the manifold nervous mechanisms of the lower tegmental region; and indeed there exist definite connections of the auditory fibres with the pons and bulb, connections serving not for the elaboration of auditory impulses but for bringing those impulses to bear on motor mechanisms, connections which for simplicity's sake we have omitted to describe.

Perhaps the more important of these lower connections of the auditory fibres are those with the corpora quadrigemina, by means of which in the absence of distinctly psychical events auditory impulses can bring forth bodily reactions, such as movements and the like, of a complicated kind. The striæ acusticæ moreover, as we have seen, are connected with the cerebellum.

It is interesting to note that as the optic tract contains efferent fibres carrying, presumably, centrifugal impulses from the anterior corpus quadrigeminum, and the olfactory tract similar efferent fibres, so also the auditory nervous mechanism possesses efferent fibres. These pass from the posterior corpus quadrigeminum or from the lateral fillet nucleus by the lateral fillet, and thence either by the striæ acusticæ or the trapezoid fibres to the tuberculum acusticum and accessory nucleus of the opposite side. The purpose of these efferent fibres in the various sensory mechanisms has not been as yet clearly made out, but possibly they may be used to exert either an augmenting or an inhibitory influence on the recipient elements of the sense organ.

We have now to enquire how far experiment and clinical study corroborate the conclusions which may thus be drawn from anatomical relations. What is the effect, for instance, of removing in an animal, the temporal convolutions on one side or on both sides? We may here in the first place remark that in view, on the one hand, of the auditory tract being in part only a crossed one, and on the other hand, of the great difficulty in distinguishing the effects of hearing with one ear only from those of hearing with both ears, relatively little importance can be attached to the experiments in which one hemisphere only is operated on. In the second place the effects of sound on the animal body are so manifold, the responses which the nervous system makes to auditory impulses are so varied and often so delicate, that it becomes a matter of extreme difficulty to decide whether an animal operated on does or does not retain distinctly psychical auditory sensations. It does not follow, for instance, because an animal starts at a sound that it really "hears." In spite of these difficulties however there seems to be increasing evidence that removal of the temporal convolutions, especially of the superior temporal convolution, does do away with distinctly psychical auditory sensations.

We saw in dealing with visual sensations (§ 67) that the visual area in the cortex was directly connected by efferent fibres with the mechanisms for the movements of the eyes and thus explained why stimulation of that area produced those movements. There appears to be a similar connection by similar direct efferent fibres between the superior temporal convolution and the nervous mechanisms for the movements of the ears, head and neck associated with hearing. When in the monkey this cortical region is stimulated the animal pricks its ears as if it heard something. This is evidence of an indirect kind in favour of the special auditory function of the convolution.

Of more value perhaps than the results of experiments on animals, in spite of the frequently diffused character of the lesions of disease and the occurrence of complications, are the results of clinical study; and these point more and more distinctly to the cortex of the superior temporal convolution as being concerned in the development of auditory sensations. In certain cases of cortical epilepsy the warning takes on the form of an auditory sensation, a sound or noise; and in such cases this region of cortex has been found to be diseased. Disease of the same region has always been found to be accompanied by some form of deafness. In certain cases the deafness has been ordinary deafness without any adequate cause being discovered in the ear and in regions of the brain lower than the hemisphere. In other cases, crude sensations have remained, but the psychical intellectual elaboration of these has failed. Such in particular are the cases of "word deafness" to which we referred in speaking of asphasia; in this affection sounds are heard but the spoken word is not appreciated. For instance the patient, when a spoken question is put to him, though he is all attention, cannot understand it, and asks that it may be written down; seeing the written question he understands and answers. And doubtless the work of this part of the cortex like that of the visual cortex is very complex, though to a less degree. Granted that even the crude conscious sensation needs cortical elements for its development, we should expect to find that other and neighbouring elements were concerned in elaborating this crude sensation into a higher perception and eventually into an idea. But we must not here attempt to deal with this part of the subject.

SEC. 9. ON THE DEVELOPMENT OF CUTANEOUS AND SOME OTHER SENSATIONS.

§ 678. The sensations with which we have just dealt arise through impulses passing along special nerves or parts of special nerves, the optic nerve, the olfactory nerve &c.; we have now to deal with sensations arising through impulses along the nerves of the body generally. These are of several kinds. In the first place there are sensations which we may speak of as "cutaneous sensations," the impulses giving rise to which are started in the skin covering the body, or in the so-called mucous membrane lining certain passages. These sensations, which as we shall see in dealing with the senses are dependent on the existence of special terminal organs in or near the skin, are sensations of "touch," in the narrower meaning of that word, by which we appreciate contact with and pressure on the skin, and the sensations of "temperature," which again we may, as we shall see, divide into sensations of "heat" and sensations of "cold." These sensations may be excited in varying degree by impulses passing along any nerve branches of which are supplied to the skin. Then there are the sensations constituting the "muscular sense," to which we have already referred, and these again may be excited in any nerve having connections with a skeletal muscle.

As we shall see in dealing with the senses, when a sensory nerve is laid bare and its fibres are stimulated directly, either by pressure, such as pinching, or by heat, or by cold, or in other ways, the sensations which are caused do not enable us to appreciate whether the stimulation is one of contact or pressure, or of temperature, or of some other kind; we only experience a "feeling," which at all events when it reaches a certain intensity we speak of as "pain." And we have reason to think that at least from time to time impulses along various nerves give rise to sensations which have been spoken of as those of "general sensibility," by which in addition to other sensations, such as those of touch and of the muscular sense, we become aware of changes in the condition and circumstances of our body. When the stimulation of the skin exceeds a certain limit of intensity, the sense of touch or temperature is lost in, that is to say, is not appreciated as separate from the sense of pain; and under abnormal circumstances acute sensations of pain are started by changes in parts, for example tendons, the condition of which under normal circumstances we are not conscious of appreciating through any distinct sensations, though it may be that these parts do normally give rise to feeble impulses contributing to 'general sensibility.' It may therefore be debated whether 'pain' is a phase of all sensations, or of general sensibility alone, or a sensation *sui generis.* We shall have something further to say on this matter when we treat of the senses; meanwhile it will be convenient for present purposes if we consider that the sensations we have to deal with just now are the sensations of touch and of temperature, those of the muscular sense, and those of general sensibility, including those of pain.

§ **679.** It will be advisable to treat of these several sensations in the first instance together; we may subsequently attempt to ascertain how far they differ from each other in their mode of development.

Let us first turn to the indications afforded by anatomical arrangements; and we may in this confine ourselves chiefly to the spinal nerves, since these are by far the more numerous. Calling to mind what was said in former chapters concerning the structure of the spinal cord and bulb, we are struck by the fact that the paths of sensory impulses indicated by the connections of the dorsal roots of the spinal nerves while in part they lead up towards the cerebral hemispheres, also and indeed conspicuously lead to the cerebellum. Now all the evidence obtainable justifies us in concluding that the integrity of the cerebral hemispheres and of their connections with other parts of the central nervous system is essential to development of complete and perfect sensations; in order that a cutaneous sensory impulse may give rise to a fully developed cutaneous sensation it must have access to and bring into activity the cerebral cortex. There is no analogous evidence in respect to the cerebellum; on the contrary, all the available evidence shews that the cerebellum cannot by itself develope sensations. Its intervention in the general mechanism of sensations is an indirect one only. The sensory impulses which reach and affect the cerebellum do not give then and there rise to sensations; they can produce these only by means of some subsequent activity of the cerebral hemispheres, with which as we know the cerebellum is connected. We may conclude that the sensory impulses which pass to the cerebellum take that route for some special purpose; and the persistence of cutaneous and other sensations, after removal of cerebellum or extensive disease of it, shew that its activity, whatever that special purpose may be, is not essential to the mere development of sensations out of sensory impulses. We may consider the cerebellar path of sensory impulses, apart by itself, as something added to the direct path of those impulses to the cerebral cortex.

Confining ourselves in the first instance to the latter path we find that this is at least twofold.

In the first place, a path, conspicuous for the distinctness with which it can be made out, and yet the channel of relatively few impulses, and those probably of a special kind, is furnished by those fibres of the dorsal roots which running up the posterior columns reach and form synapses with the cells of the gracile and cuneate nuclei (which we may call together the dorsal nuclei) of the bulb, the latter receiving fibres, chiefly at all events, from the upper spinal nerves, the former from the lower. The roots of the nerves supplying the lower limb contribute very largely to the tract of fibres ending in the gracile nucleus, and the corresponding roots of the nerves of the upper limb very largely to that ending in the cuneate nucleus; but other roots apparently contribute, though to a much less extent, to the path leading to the nuclei, the thoracic roots, and those lower than these passing through the median posterior column to the gracile nucleus, and the cervical roots through the lateral posterior column to the cuneate nucleus. From the cells of both these nuclei fibres, as we have seen, crossing in the so-called sensory decussation, pass by the inter-olivary layer to the fillet of the opposite side, and so travel upwards. We may assume that the sensory impulses which travel up the posterior columns, undergoing during their passage in those columns no other change than that which an impulse can undergo while it is travelling along an axon, reach the dorsal nuclei of the bulb, and there start new impulses which travel upwards chiefly by the fillet of the opposite side. We say 'chiefly' because some fibres of the nuclei pass apparently into the fillet of the same side, and again, either by the main axons of fibres leaving the nuclei or by collaterals, impulses may be led not into the definite tract which we call the fillet, but into what at present we may call the general reticular formation of the bulb. Tracing the fillet forwards we find that the fibres from the nuclei, keeping to the side to which they have crossed, occupy the median division of the fillet, or the median fillet as it is called, and end chiefly at least in the optic thalamus. There is evidence however that some, though not a large proportion of the fibres of the median fillet, are continued on directly to the parietal cerebral cortex, passing through or behind the lenticular nucleus. Assuming that these particular fibres are the axons of cells in the dorsal nuclei of the bulb, they afford a narrow, we may say a very narrow, but very direct path for sensory impulses to the cortex, with a relay only in the dorsal nuclei of the bulb. A broader path is furnished by the fibres which end in the thalamus. From the thalamus, as we have seen (§ 633), fibres pass to the cortex, and sensory impulses taking this path reach the cortex, after having undergone two relays, first in the dorsal nuclei of the bulb, and secondly in the thalamus. By each of these paths the cortex reached is that of the hemisphere of the side of the body opposite to that on which the dorsal roots entered the cord; but, as we have said, some few of the fibres from the dorsal nuclei of the bulb may pass into, and hence some few of the impulses pass along the fillet of the same side and so reach the hemisphere of the same side unless they cross later on in their way. This path of the fillet is the main way to the cortex for sensory impulses travelling along the posterior columns to the dorsal nuclei of the bulb, though we ought not to ignore the impulses which may pass, probably through a series of relays, through the reticular formation of the tegmental region.

In the second place, another path or other paths, though less distinct and conspicuous, must be taken by the greater number of the sensory impulses which enter the cord by the dorsal roots. As we have seen, the fibres of the dorsal root end to a large extent by forming synapses, either through the main axon (or rather the two main divisions of the axon), or through collaterals with cells of the grey matter not far from the entrance of the root, and chiefly, though not exclusively, on the same side. We might imagine that axons from these cells would form an easily recognized tract of fibres proceeding directly upwards to higher parts of the brain, on their way to make connections with the cortex. But at present only a relatively few such fibres can be traced. These contribute to form the antero-lateral ascending tract, but only a small part of that tract, and moreover the tract, not of the same, but of the opposite side; crossing over in the ventral commissures to the other side, they may be traced through the bulb to the median fillet of that side, and so to the optic thalamus or other tegmental structures. Such fibres supply a path for relatively few impulses; so far as our present knowledge goes the sensory impulses which impinge on the cells of the grey matter travel for the most part upwards towards the cerebral hemispheres by the fibres, which do not, after section of or injury to the cord, appear as long tracts of degeneration but running a short course only in the white matter return to the grey matter to form fresh synapses. These impulses therefore can reach the cerebral hemispheres only after a series of relays; but the several connections by means of which they are carried to the tegmental region, and so on to the cortex, is not at present known. Some of these fibres keep to the same side of the cord as that of the cell from which they start, but many cross over to the opposite side. It must be also remembered that a path still more broken by relays is open for sensory impulses within the grey matter itself. As we have seen, the spinal cord contains cells of Golgi, each of which by its branching dendrites and branching axon brings cells into touch with cells. By means of these cells sensory impulses may be supposed to travel along the grey matter itself, and so eventually to reach the tegmental or other regions, from which they can pass to the cerebral hemispheres.

It is strange, but yet true, that while the main direct path to the cerebral hemispheres for sensory impulses is thus obscure, the paths to the cerebellum are obvious and distinct.

In the first place, in the region of the cord in which the vesicular cylinder is prominent, a considerable number of the fibres of the dorsal roots end by making synapses with the cells of the cylinder; in other regions of the cord they similarly join corresponding cells. From these cells axons proceed, as we have seen, to constitute the direct cerebellar tract which passes by the restiform body of the same side to the cerebellum. In the second place, the greater part at all events of the antero-lateral ascending tract ultimately reaches, as we have seen, the cerebellum by the somewhat roundabout pathway of the superior peduncle; this also keeps to the same side. Thirdly and lastly, as we have seen, fibres from the dorsal nuclei of the bulb reach the cerebellum by the inferior peduncle, chiefly passing to the same side but some crossing over to the opposite side. Thus the sensory impulses which reach the cord by the dorsal spinal roots, whether they travel along the posterior columns to the cells of the dorsal nuclei of the bulb, or to the cells of the vesicular cylinder, or to those cells in the grey matter of the cord which give rise to the fibres of the ascending lateral tract, all reach or have an opportunity of reaching the cerebellum, and, we have reason to believe, the superficial grey matter of that body, the majority of the impulses at all events reaching the cerebellum of the same side. Each half of the cerebellum is connected with the opposite cerebral hemisphere, on the one hand through the middle peduncle and the pons, and on the other hand through the superior peduncle. We shall discuss the meaning of these connections later on; meanwhile we may note that by these two ways the events in the cerebellum, whatever be their nature, which result from the influence of sensory impulses, are brought into relation with the cerebral cortex; and while the sensory impulses which influence one half of the cerebellum are those brought chiefly by the dorsal roots of the same side, the relations of each half of the cerebellum are with the cerebral hemisphere of the opposite side.

§ 680. Thus the several possible paths towards the cerebral cortex for sensory impulses which started in the skin and other tissues enter the cord are as follows:

1. A special and very limited path by the posterior columns in which no relay is met with until the bulbar nuclei are reached. That relay however is an extensive and a remarkable one. When the degenerating tract in the median posterior columns due to the severance of a single root, for instance the 6th lumbar root in the monkey, is traced up into

the gracile nucleus, it is observed to spread out very widely within the nucleus. That is to say, within the nucleus there appears to take place a very great dispersal and commingling of possible paths for the passage of impulses. And a like dispersal probably takes place in both the nuclei in respect to all the fibres from the dorsal roots which reach them. We may conclude that business of no little importance is carried on in these nuclei of the bulb. From this relay some few of the impulses, modified we may assume by the cells of the bulbar nuclei, may travel onward direct to the cortex by that small portion of the fillet which appears to pass to the cortex, through the lenticular nucleus, without any break occasioned by synapsis. But the majority of the impulses travelling along the fillet impinge on the cells of the thalamus or adjoining tegmental structures, and only reach the cortex after a relay, and probably a modification of their nature in these tegmental bodies. Most of these impulses thus travelling along the fillet cross from the bulbar nuclei to the opposite fillet, and so reach the opposite cerebral hemisphere. It may be added that possibly some impulses leaving the bulbar nuclei pass not into the fillet but into the reticular formation of the bulb, and by it, or by paths not as yet known but probably marked by relays, work their way along the tegmentum and from it reach the cortex.

2. A path which is probably a more general path, the first relay of which takes place in the cells of the grey matter of the cord not far from the entrance of the root along which the impulses have reached the cord. Some few of the impulses taking this course travelling along fibres which, crossing in the ventral commissures, join the antero-lateral ascending tract of the other side, appear to pass up to the thalamus or other tegmental structures until they meet with a relay, whence they are carried to the cortex. But for the majority of the impulses passing from the said cells of the grey matter towards the cerebral hemispheres no such long tract of fibres is provided. No particular path is marked out for them by our present knowledge. They may travel by the short fibres spoken of above, meeting with frequent relays, and finally reach the tegmental region of the bulb, and so that of the pons and crus; many of these apparently cross to the opposite side. Or their path may be absolutely confined within the grey matter, in which case their journey would seem to be a long series of repeated relays. In both cases the impulses reach the tegmentum, and pass thence to the cortex.

3. The superadded cerebellar path. This is provided by fibres from the bulbar nuclei to the restiform body for the impulses which take the more special path by the posterior columns, and by the fibres of the direct cerebellar tract and a large part of the antero-lateral ascending tract for the impulses which are, so to speak, let loose upon the cord soon after their

entrance into it. In both cases the impulses are at all events chiefly gathered up from the same side of the cord. The events in the cerebellum to which these impulses give rise are by the middle or by the superior cerebellar peduncle brought into relation with the opposite cerebral hemisphere.

All the sensory impulses, with the exception of the few which may travel by the cerebral continuation of the fillet, find their way ultimately to the tegmental region (including in that term the thalamus), whatever be their earlier path, and it is from relays in the tegmental region that they are able to affect the cerebral cortex.

It may be interesting to compare with these paths of sensory impulses coming up by spinal roots what is known of the path open for sensory impulses,reaching the central nervous system along the cranial nerves. We may take as an instance the trigeminal. We have traced the sensory fibres of this nerve into its sensory nucleus, and into the gelatinous substance accompanying the so-called 'ascending' root; here they end by making synapses. From the cells of the gelatinous substance, if not also from the sensory nucleus axons proceed which crossing the median raphe become constituent fibres of the opposite median fillet. Other axons, as well as some of the numerous collaterals given off by the above axons, appear to end in the reticular formation; and for such sensory impulses as pass along these, no path towards the cerebral hemisphere is at present known, other than a general path through the tegmental grey matter. It may be added that some observers have described fibres connecting the sensory nucleus of the trigeminal with the cerebellum, but this does not seem certain. From what has been said however it will be seen that this cranial nerve resembles the spinal nerves in having a special path by the fillet and a more general path by the tegmentum. And the same may be said of the other sensory cranial nerves.

There remains to inquire what anatomical evidence has to say concerning the regions of the cortex especially connected with the sensory paths which we have thus traced to the tegmentum. The connections of the cerebral cortex with the tegmentum are very complex, fibres pass from many parts of the one to the other; but such evidence as is available seems to point to that part of the cortex which we have already called the Rolandic area as the region in question. To this region also passes the direct cerebral continuation of the fillet. Injury to the tegmentum, and especially to the optic thalamus, causes a degeneration ascending to this region. Conversely removal of the region in the young leads to atrophy of the optic thalamus and other tegmental structures, and also it is said of the median fillet, and even the nuclei of the bulb. Further, the myelination of the fibres of the pyramidal tract descending from this area is preceded by the myelination of other accompanying fibres which may be traced, not like the pyramidal fibres to the pes but to the optic thalamus and other parts of the tegmentum, including the fillet, and which may be considered as carrying impulses to the cortex.

§ **681**. We may now turn to what can be learnt by experiment and clinical observation.

Clinical experience shews that in man the integrity of the cerebral hemispheres, and of the connection of the hemispheres with the rest of the central nervous system, is essential to the full development of sensations; and that in this respect each hemisphere is related to the crossed side of the body. A very common form of paralysis or "stroke" is that due to a lesion of some part of one hemisphere (the exact position of the lesion need not concern us now), frequently caused by rupture of a blood vessel, in which the patient loses all power of voluntary movement and all sensations on the crossed side of his body (including the face); he is said to be suffering from hemiplegia, "one sided stroke." Not only do voluntary impulses fail to reach the muscles of the affected side, but sensory impulses, such as those which, started for instance in the skin, would under normal conditions lead to sensations of touch, of heat or cold, or of pain, fail to effect consciousness, when they originate on the affected side; the patient cannot on that side feel a rough surface, or a hot body, or the prick of a pin. For the sake of clearness we have spoken of the loss of movement and sensation as complete, but it might of course be partial; and indeed a complete loss of all sensation of pain is extremely unfrequent, if it ever occurs at all; but we are not now attempting to distinguish between the various kinds of sensation.

Experiments on animals, so far as they go, lead to the same conclusion, namely, that the integrity of the cerebral hemisphere, we may say of the cortex of the hemisphere, and of its connections with the parts below is essential to the full development of sensations started by stimuli applied to the opposite side of the body. That is to say, sensory impulses reaching the spinal cord by one of the spinal nerves, or the lower brain by one of the cranial nerves, cross over somewhere to the opposite side and do not become developed into full and perfect sensations until they have in some way called into play the cortex of the opposite hemisphere. We may here, in passing, repeat the warning which we have already given as to the extreme difficulty of drawing conclusions concerning the sensations and feelings of an animal, seeing that in so doing we are limited to purely objective signs. We can in most cases ascertain whether an animal is feeling pain or no, though even in this we may be misled; but when we attempt to judge whether an animal really appreciates the nature or even the intensity of a sensory impulse generated say in its skin, we have very scanty and uncertain guidance. Hence, in these matters clinical observations on man, who can more or less successfully describe what he feels, are of predominant value in spite of all the difficulties attendant on them.

In discussing voluntary movements we came incidentally to the conclusion that the Rolandic area is in some way connected with the sensations of which we are now treating. The evidence of this is briefly as follows. The parts of the body, movements of which are produced by stimulation of the cortex in this area, are 'represented' as is said in the cortex, are endowed with sensibility, and the cortical representation of a part is proportionate to the sensibility no less than to the mobility of the part; the parts which are highly sensitive, such as the hand, are represented by relatively large areas of cortex, those which are little sensitive, such as the back of the trunk, by small areas. Removal of the cortex in an animal affects sensation, no less, indeed somewhat more than movement. In epileptic attacks of cortical origin, a sensation, the aura, precedes the movement; and the man, whose cortex is stimulated while he is conscious, describes a sensation as the dominant effect.

Putting this experimental and clinical evidence side by side with the anatomical evidence referred to above, we are led to the conclusion that the sensations with which we are now dealing are developed through the activity of the cortex in the Rolandic area out of sensory impulses which are brought to bear on that cortex through the fibres connecting that cortex with the thalamus and other tegmental structures. This conclusion is supported by the clinical experience that a lesion interrupting these fibres results in loss of sensation, anæsthesia, in the opposite side of the body.

But this is not the whole of the matter. The large gyrus fornicatus (Figs. 133, 135) on the mesial surface lies wholly outside the Rolandic area, being separated from it by the callosal-marginal sulcus. Stimulation of the cortex dorsal of this sulcus produces, as we have seen, movements of the trunk and other parts, but stimulation of the gyrus fornicatus ventral of the sulcus calls forth no movements whatever. Yet in the hands of more than one observer, the destruction of the whole or even of a part of this convolution in the monkey has led to a complete loss of sensations on the opposite side of the body, and that without loss of voluntary movement. The operation is a difficult one, but there are no valid reasons for thinking that the very obvious and unmistakeable loss of sensation following the operation was due to incidental damage of other parts. It seems impossible to resist the conclusion that this part of the cortex is in some way or other connected with the development of cutaneous sensations.

It will not be profitable to discuss here what are the relations of the activity of this convolution to the activity of the Rolandic area as regards the development of sensations. There is no evidence at all that the several parts of the body are represented topographically in the gyrus fornicatus as they are in the Rolandic area; hence its activity as regards sensation must be of a different kind from that of the Rolandic area. But our present knowledge does not enable us to state anything as to the exact nature of that activity. We cannot suppose that the destruction of the gyrus fornicatus produces anæsthesia by annulling the sensory activity of the Rolandic area, since voluntary movements continue, and these, as we have seen, are contingent on sensations. But if the Rolandic area remains functionally active as regards sensations, how is it that the injury to the gyrus fornicatus can possibly produce loss of sensations? Obviously the matter is one of great complexity.

The events in the cortex, whether of the Rolandic area or of the gyrus fornicatus, which issue in conscious sensations, are the result of influences brought to bear on the cortex through changes in the tegmental structures. What is the nature of these changes, and what name shall we apply to them? We shall probably not go far wrong if relying on the analogy of the mechanism for visual sensations we speak of these tegmental structures as lower sensory organs. The tactile and other sensations with which we are now dealing probably need less elaboration than do visual sensations, but we may take it for granted that they need some. Even less however than in the case of visual sensations can we state what is the nature of that elaboration. We have seen that in the lower animals at all events elaborated sensory impulses, whether we call them sensations or not, are busily at work in the complete absence of the cerebral hemisphere; and we may probably conclude that the nervous machinery for the elaboration and direction of such impulses is to be found in these tegmental structures. Further, if in such higher animals as man and the monkey, the working of such elaborated impulses seems absent, it is because in these organisms the welfare and activity of the machinery through which they work is so closely dependent on the coincident integrity and activity of the cortex.

§ **682**. Here we may fitly introduce what we have to say concerning the different kinds of sensations experienced by means of the skin and other general tissues of the body, and their individual development. In the case of visual sensations, as we shall see when we come to treat of these in detail, we have to do with two characters only. When a pencil of rays from a luminous point falls on the retina we are aware in the first place of the quality of the sensation, the luminous point appears of a certain brightness and of a certain colour, and in the second place of the relations in space of the sensation to other possible visual sensation, the point occupies a certain position in our field of vision. The visual nervous machinery has to provide for both these things. As we have seen, the retina is probably in some way or other topographically represented in the visual machinery; and each portion of the machinery, we may, for simplicity's sake, without committing ourselves say that each area of the cortex thus correlated to a particular area of the retina can be the instrument for the development of several sensations which differ from each other as to quality but occupy the same position in the field of vision. We may compare the skin and other tissues from which sensory impulses proceed with the retina and regard it as supplying a field of sensations comparable to the field of vision, the constituent parts of the field not being however parts of external space but of our own body. Thus when a hot body or a cold body is brought in contact with or even sufficiently near to the skin of the tip of the right forefinger we have a sensation of heat or of cold, and at the same time we are aware that we have gained that sensation by means of the tip of the right forefinger. We localize the sensation at the same time that we appreciate it; we refer it as it is said to a particular region of the body. And this feature of localization pertains to all the sensations with which we are dealing, though in different degree. The power of localization is most marked in the case of the sensations of touch proper and of temperature; it is less marked in sensations of pain, and still less in the sensations which we have spoken of as those of general sensibility and in those which go to make up the 'muscular sense'; the latter are in this respect much more diffuse, much less exact than the former. This localization, as we shall see, is unequal as regards different parts of the body; it is for instance much more exact in the fingers than in the back, and the distribution of exactitude is not the same for all sensations, is not exactly the same for instance in sensations of touch as in those of temperature. For the purposes of life this power of localizing a sensation is as important as, perhaps more important than, the appreciation of the intensity of the sensation; and usually we speak of a part, such as the tip of the finger, as being very sensitive when the power of localizing is very highly developed.

By means of the nerves proceeding from the tip of the finger we have then several distinct kinds of sensations which we all recognize as coming from the tip of the finger; these we distinguish as sensations of touch, of heat, of cold and of pain (we may for simplicity's sake limit ourselves to these), and we can recognize degrees in each. We may safely assume that a special nervous mechanism of some nature or other is provided for each kind of sensation. We may probably also assume that in each case a special kind of peripheral beginning, what we may broadly call a peripheral organ, is provided, as also a special kind of central ending. We may probably go so far as to assume that the sensory impulses giving rise to the sensation travel in each case along special channels, that is to say, along special fibres. But we are not justified in assuming *à priori* that the several different paths suggested by anatomical arrangements correspond to the different kinds of sensation, so that the sensory impulses of one kind travel along one path, and another along another. It may be so or it may not be so; observation can alone decide.

§ **683**. Clinical histories make it very clear that special nervous mechanisms for the several kinds of sensation do exist. Sensations of touch may be interfered with or even annulled, while those of pain remain intact or almost so, and *vice versa*. Thus cases occur in which a needle may be thrust into the skin without any pain being felt, though the patient is aware that a needle is in contact with a particular spot of the skin, and others in which pain has been felt upon the insertion of a needle, though mere contact of the needle or ordinary pressure with it could not be appreciated. Again, sensations of touch proper, tactile sensations produced by contact and pressure and sensations of temperature may be affected independently. The muscular sense also may be affected apart from other sensations. Further, these differences have been observed not in cases of cerebral disease only but also in cases of spinal disease; that is to say, the differences in the ultimate conscious sensations may be brought about by interfering with the sensory impulses while they are as yet on their way towards the brain; this affords strong presumption that the several kinds of sensory impulses follow separate paths.

But neither clinical study in man, nor experimental observation on animals, enables us at present to make any distinct statement as as to what those paths are. It might be supposed that the very distinct path by the posterior columns, bulbar nuclei and fillet serves as the special path for a particular kind of sensation; and the kind of sensation which naturally suggests itself as the one taking this path is the highly localized tactile sensation proper. But neither the clinical cases in which disease is limited to the posterior columns, nor the observation of the behaviour of animals in which the posterior columns have been divided, afford adequate proof that such a view is true. If tactile sensations travel alone and exclusively by the path in question, then a block in the median posterior column, say in the thoracic region, which would leave the root-zone in the lateral posterior column untouched, ought to abolish tactile sensations in the parts below, leaving other sensations unaffected. But it does not; sensations are affected but not the tactile sensations exclusively; and moreover the deficiency of all kinds of sensation is not great. We seem driven to the conclusion that sensory impulses in general pass upwards towards the brain, not by the special path of the posterior columns or not by this alone but chiefly by the more general path which we described a little way back; if the impulses taking this course reach the cerebral hemispheres by way of the fillet they must find their way to the fillet by some tract other than that supplied by the fibres from the bulbar nuclei. This conclusion is confirmed by the results of experiments on animals. Sensation as a whole is more interfered with by division of the lateral, especially the antero-lateral columns of the cord, than by the division of other parts. Further, both experiments on animals and clinical observations tend to shew that sensory impulses cross largely, even if gradually and tardily, to the other side of the cord, on their way to the brain. This, as we have seen, corresponds to the anatomical feature of what we have called the more general path, whereas the special tract by the posterior columns does not decussate until the bulbar nuclei have been passed.

Again, seeing that the cerebellum seems in some special way connected with the coordination of movements, it is tempting to suppose that the cerebellar tracts, possibly more particularly the direct cerebellar, serve as the path for the sensory impulses giving rise to the muscular sense. But, again, clinical and so far as it goes experimental evidence gives no adequate support to such a view.

§ **684.** In the present state of our knowledge, then, the results of clinical study and experiment, while they confirm the view as to the passage of sensory impulses upwards along the cord suggested by the anatomical arrangements do not enable us to say which of the paths is taken by a particular kind of sensation; indeed they rather raise the suspicion that the existence of more than one path along the cord has to do with the passage of sensory impulses of all kinds and has some other meaning. We may extend this view to the path beyond the cord within the brain. There we have to do with the limited and well-marked path by the median fillet and a more general, at present undefined path by other parts of the tegmental region. We have at present no satisfactory clinical or experimental evidence that the fillet serves for a particular kind or for particular kinds of sensations exclusively. Nor is there adequate evidence that it alone serves as the sole channel for those sensory impulses which are about to be developed into conscious psychical sensations, all other sensory impulses spending themselves upon the lower machinery of the middle brain. That the median fillet is in some way most important for the development of sensations seems very certain, but we are not as yet in a position to state definitely what part it exactly plays.

It may be worth while in this connection to compare the cutaneous and other sensations on which we are now dwelling with visual sensations. When a luminous point gives rise to visual sensations, these may be of quite different kinds. A sensation of white light and a sensation of red light (or say of red light and of blue) are as different from each other in kind as are a sensation of a prick and a sensation of a burn. Now though there are at least two quite distinct paths to the cortex, that by the pulvinar and that by the corpus geniculatum, it has never even been suggested that one serves for one kind of visual sensation, and the other for another. Yet there must be a meaning for these two separate paths, and when we have discovered that meaning, we shall probably see our way to explain the separate paths for cutaneous sensory impulses.

Again, there is no evidence whatever which would lead us to suppose that the visual impulses giving rise to a red sensation are carried to a particular part of the cortex, and those giving rise to a blue sensation to another part. The only topographical distribution in the cortex is one corresponding to the field of vision, and the differentiation of the several kinds of visual sensations derived from the same part of the retina is probably effected by a finer sort of machinery distributed generally, even if not uniformly, over the whole cortical area concerned in the development of visual sensations. And probably the same holds good for cutaneous sensations.

The meaning of the remarkable cerebellar grip on the path of sensory impulses had better be left until we come to speak of the cerebellum as a whole.

§ **685**. We have purposely said very little, and that for the most part incidentally, as to the results of the experiments in the way of hemisection or other partial section of the spinal cord in animals, on which in times past much stress has been laid, and concerning which much discussion has taken place. Their value in view of our main topic, the development of sensations in man, is limited; not in the downward centrifugal path of the pyramidal tract only, but also in the features of the upward, centripetal paths does the spinal cord of a rabbit or a dog differ greatly from that of man; the posterior columns of the cord like the pyramid tract are more highly developed in the higher animals.

The results of such experiments may be briefly summarized as follows. Hemisection of the cord in a dog produces as an immediate effect a loss or great diminution of sensation, not only on the same side but also on the opposite side; but these effects after a while pass away so largely that permanent defects of sensation can with difficulty, if at all, be detected. This recovery may be interpreted as due on the one hand to the passing off of the effects of the operation, the shock and the like on which we have more than once dwelt, and on the other hand to the establishment of new vicarious paths for the sensory impulses. Further, if after a hemisection at a certain level, with subsequent recovery a second hemisection higher up on the opposite side be performed, this is followed like the first by loss or great impairment of sensation, and like the first may be followed by recovery or at least great improvement. Even a third hemisection, still higher up, on the same side as the first may be performed, and yet a large amount of recovery may take place.

In such cases the sensory impulses must travel in a zigzag manner from side to side, passing across the breaks made by the hemisections, either by the short course fibres of the white matter, or simply by the grey matter from cell to cell. Such experiments throw, however, but little light on the normal passage of sensory impulses in the highly-strung spinal cord of man; they only illustrate what we know in other ways, as by the strychnia experiments (§ 586) that in the complex labyrinth of the cord, the path taken by an impulse among many anatomical possibilities is determined by physiological conditions. That such vicarious action as is shewn in the case of the dog, is very rarely, if at all, seen in the monkey and not at all in man, is to be explained by the greater dependence of the welfare of spinal elements in these more highly organized beings on the normal influences exerted on them by the brain (cf. § 658).

It may be interesting to note that in a dog which had partially recovered voluntary movements in its hind limbs after a third hemisection of the thoracic cord, when, at its death, a strong tetanizing current was directed through the bulb and cervical cord no movements of the hind limbs followed; the impulses started by artificial stimulation could not pass the bridge which sufficed for volitional impulses of natural origin. We have no reason to think that the failure was due to diminished irritability consequent on death; we should rather take the result as a warning against assuming that the 'nervous impulses' which sweep naturally up and down the central nervous system are identical in nature with those started in peripheral nerves by artificial stimulation.

Experiments on animals have also shewn that the upward paths for sensory impulses lie largely in the antero-lateral columns; the afferent impulses affecting the bulbar vaso-motor centre, for instance, seem to travel in this column; but the experiments throw little light beyond that which we have already otherwise gained.

One phenomenon perhaps deserves mention. In some cases hemisection of the cord, while causing loss or impairment of sensation on the opposite side, brings about an increase of sensibility, a 'hyperæsthesia' of the same side. The hemisection causes loss of vaso-motor tone on the same side, and this by increasing the sensitiveness of the peripheral sensory organs may be the cause of an apparent but not real increase in the facility with which sensory impulses travel along the cord. This however we cannot regard as the whole explanation; vaso-motor tone is soon reestablished, whereas this hyperæsthesia persists for a very long time, and probably never passes off, though it may vary in intensity from time to time. It may perhaps be compared with the increased sensitiveness which is observed when in dividing separately a series of sensory spinal roots an area of sensitive skin is left surrounded by insensitive areas; the sensitiveness of that area appears to be heightened. In both cases the increase of sensation is most marked in the parts of the sensitive area bordering on insensitive areas. We may also compare this hyperæsthesia with the increased briskness of the knee-jerk which results from the severance of the sensory nerves adjoining those necessary for the knee-jerk mechanism. When we come to deal with vision we shall have to study the phenomena of 'contrast'; we shall see that stimulation of a limited area of the retina in producing its effects on the corresponding part of the cerebral visual mechanism also produces effects of an opposite character in neighbouring parts of that mechanism. The hyperæsthesia which we are considering appears to belong to this class of phenomena. Its occurrence warns us that while we must admit the conclusion that sensory impulses coming from one side of the body are developed into sensations in the opposite cerebral hemisphere, we must not assume that the other hemisphere is not in any way affected by them and has nothing whatever to do with them. We ought perhaps to conclude that in every cerebral act both hemispheres are always at work, though in different ways.

§ **686**. We may now briefly sum up the conclusions arrived at in the preceding discussions somewhat as follows.

The several cutaneous and other sensory impulses carried to the spinal cord by the dorsal spinal roots travel up the cord by more than one path. There is a special path by the posterior columns leading by the bulbar nuclei chiefly to the fillet of the other side, and so to the thalamus and adjoining tegmental structures, some few of the impulses apparently reaching the cortex directly by the cerebral continuation of the fillet. The other path is a more general path by way of cells of the cord placed not far from the entrance of the root. Thence a somewhat narrow path is afforded by fibres which, crossing over to the antero-lateral tract of the opposite side, pass on through it to the fillet. The path of the remaining impulses upwards towards the cerebral hemispheres is not exactly known; they do not follow long tracts which reveal themselves by degeneration; they may pass by relays along fibres of short course or may travel by more frequently repeated relays along the grey matter; they appear gradually to cross over to the opposite side, and may be regarded as ending in the tegmentum, whatever be the way by which they reach it. In like manner the sensory impulses reaching the central nervous system along the sensory cranial nerves pass upward on the one hand by the fillet, and on the other hand by the more general path of the tegmentum.

From the tegmentum the various sensory impulses pass to the cerebral cortex, to that of the Rolandic area, and apparently to that also of the gyrus fornicatus; and in the cortex they are developed into full sensations. But how the events in the gyrus fornicatus differ from those in the Rolandic area, and how these are related to each other, is not known. While passing along the tegmental region the sensory impulses are brought into connection with the complex nervous machinery of the middle brain and thus serve for carrying out such effects of sensory impulses as can be carried out in the absence of the cerebral hemispheres.

Though obviously the several kinds of sensory impulses both travel in the cord and are developed in the brain in such a way that by disease or otherwise they may be affected separately or differently, the conditions determining their passage and development, whether for instance they travel along separate tracts, cannot at present be definitely stated.

Lastly, a large number of impulses are carried up, not to the tegmentum and the cerebral hemispheres, but to the cerebellum, chiefly of the same side; and such share as these may have in developing or influencing conscious sensations or whatever work they may have to do is brought about through the connections of each hemisphere of the cerebellum with the crossed cerebral hemisphere.

SEC. 10. SOME OTHER ASPECTS OF THE FUNCTIONS OF THE BRAIN.

§ **687**. We may now, changing our plan of attacking the subject, attempt to form some conclusions in respect to the functions of some of those parts of the brain, concerning which the previous discussions led us to say little or nothing. We will first turn to the cerebellum, the many ties of which with other parts of the central nervous system have repeatedly come under our notice, and the complex nature of the superficial grey matter of which has already attracted our attention. In dealing with this it will be advantageous to reverse the order which we have hitherto adopted. We will consider first the results of experimental enquiries and clinical observations, and afterwards compare these with the teachings of anatomy.

Unlike the case of the cerebral cortex, electrical stimulation of the cerebellar surface has yielded results of no great importance. Movements of the eyes and other parts of the head apparently connected with vision as well as movements of the limbs obviously connected with progression have been observed, but nothing very definite has been learnt.

When in an animal, monkey, cat, or dog, for instance, the whole cerebellum is removed, and the immediate effects of the operation have passed away, the condition of the animal is such as to excite wonder that the loss of so large and apparently important organ has brought about so little change. Its psychical powers do not appear to be at all impaired or changed; it is as alert and as intelligent as before. Sight, hearing, and the other special senses, seem unaffected; there are no distinct signs of its cutaneous or general sensibility being deficient or altered. The most that can be observed is a deficiency in its movements; these are marked by a certain amount of what we may for the present speak of under the general term of 'incoordination.'

If, instead of the whole, one-half of the organ be removed, the effects of the loss can be more satisfactorily analysed; and these are found to be as follows. For convenience of description we will suppose that it is the right half which has been removed.

No change in psychical condition can be discovered; none in the development of sensations; the skin of one side is neither more nor less sensitive than that of the other. But movements are abnormal; they are not the same on the two sides of the body, and examination discloses that the difference is due to modifications of the movements of the right side, that is, of the same side as that on which the half of the cerebellum was removed. The animal uses the left side, and especially the left limbs more than the right; it moves the left limb in preference to the right, it leans towards the right side, it falls on the right side, and in general shews by the character of its movements that the muscles of the right side are not being worked in a normal manner. The condition is one not so much of absolute loss of power, as of imperfect action. This imperfect action has been described under the general term incoordination, but has been analysed, though all observers are not agreed in this, on the one hand into diminished power, that is to say, energy of contraction (parasthenia), which, in the dog, is most conspicuous in the muscles of the hind leg, and on the other hand into a diminished tone (paratonia), and an unsteadiness of contraction due to the occurrence of small and rapid, though regular tremors (parastasia). Some observers have also found evidence of a kind of overaction of the muscles on the right side, so that the neck is curved on the right side and the right limbs are stiffened; and it is stated that the knee-jerk is, after a time, exaggerated on the right side. In the dog, the diminished power over the right hind leg is often so marked that the animal has a difficulty in standing, in supporting the weight of its body; yet the diminution is not so great as to prevent the animal swimming with ease, the water affording support to its body. Obviously there is something wrong in the nervous machinery for carrying out the movements, and especially perhaps the voluntary movements of the right side. This is further shewn by the fact that the animal has a great tendency to execute one of the movements which, in an earlier part of this work, we described (§ 645) as 'forced movements'; it is apt to roll round the long axis of the body, turning from the right side to the left. Abnormal action of the ocular muscles is also, if not always, at least at times observed; the eyes are turned, 'deviated' towards the left side; but this, in some cases at all events, is repeatedly corrected as it were by jerking movements (lateral nystagmus) back towards the right side.

In the above we have supposed the right half of the cerebellum to be removed; but like results, *mutatis mutandis*, follow the removal of the left half; each half of the cerebellum has something to do with the muscular actions of the same side of the body as itself. So far as we know at present, the machinery of the skeletal muscles only is affected; there is no evidence that splanchnic movements or indeed splanchnic events of any kind are in any way dependent on the cerebellum. And we may remark in passing that the old idea of the cerebellum being especially connected with sexual functions has no real support.

The above results of experimental enquiry are in a general way supported by clinical observation. Disease of the cerebellum, uncomplicated by lesions in other parts of the brain, in no way interferes with psychical powers, and does not in the least impair sensations, either special or general; the blindness which is a symptom of tumour of the cerebellum is due to a mechanical effect of the tumour upon the visual machinery. But it does interfere with the action of the skeletal muscles. The disorder which it brings about, an unsteady gait, the 'cerebellar reel,' not wholly unlike that of drunkenness, is usually described as 'incoordination'; but, so far as it can be analysed, seems to be of the same nature as that produced experimentally in animals; the same diminution of power leading to a difficulty in maintaining the erect posture, the same diminution of tone, and the same occurrence of tremors have been observed. When the lesion is confined to one side of the cerebellum, say the right, the same deviation of the eyes to the left, and the corrective lateral nystagmus, are part of the symptoms; and a vertigo, due to things seeming to be slipping towards the right in the field of vision, as the eyes themselves move to the left, is often met with. In fact trustworthy clinical observation and experimental inquiry are in this matter singularly concordant.

What light does anatomy throw on this obvious connection between the cerebellum and the skeletal muscles, between one side of the cerebellum and the muscles of the same side?

As we have seen the connections of the cerebellum with the afferent fibres of the spinal nerves are conspicuous. The direct cerebellar tract carries impulses, after a relay by means of cells in the vesicular cylinder, or of analogous cells, up to the cerebellum by the inferior peduncle. Fibres of the ascending antero-lateral tract carry impulses, after a relay in some or other cells of the grey matter lying not far from the entrance of the nerve root to the cerebellum by the superior peduncle. Fibres passing from the dorsal nuclei of the bulb, the gracile and cuneate nuclei, carry to the cerebellum by the inferior peduncle impulses which, passing upwards along the posterior columns, have undergone a relay in those nuclei. In the case of the two former tracts the connections are wholly on the same side; the connection with the nuclei of the bulb is partly crossed, but to a large extent uncrossed. Thus, whichever be the path taken by sensory impulses as they pass into the cord, whether they make for the posterior columns, or for the cells of the vesicular cylinder, or the more general cells of the grey matter, there is a way, we may say, a broad and easy way, ready for them to the cerebellum of the same side. Probably a path to the cerebellum is present for impulses flowing inwards along the sensory fibres of the cranial nerves also, that is of the cranial nerves generally; and as we have seen there is a special connection between the cerebellum and the vestibular nerve, whether by the fibres which spring from the lateral auditory nucleus, nucleus of Deiters, as it is sometimes called, or by the fibres which pass up to the cerebellum through that nucleus without forming synapses with its cells. This connection is also a connection on the same side.

While the cerebellum has thus chiefly, though not exclusively through the inferior peduncle, ample connections with sensory elements of the same side, it has through the middle peduncle, a notable though indirect connection with the cerebral cortex of the opposite side. As we have seen (§ 632) the cortex in the frontal and occipito-temporal region is connected with the pons of the same side, through fibres which take up in the pes of the crus a position on each side of the pyramidal tract, and fibres from the parietal region, following the course of the pyramidal tract, even if we ought not to call them pyramidal fibres, also pass to the pons of the same side. From the grey matter of the pons, fibres crossing the middle line pass through the middle peduncles, which indeed they form, to the cerebellar surface of the opposite side (§ 635).

We have reason to believe that a large number of the fibres thus passing from the cerebral cortex to the pons are axons of cells in the cortex, carrying impulses from the cortex to the pons, and similarly that a large number of the fibres forming the middle peduncle are axons of cells in the grey matter of the pons of the opposite side, which, crossing the middle line, end as the 'moss' fibres or 'tendril' fibres seen in the superficial grey matter of that side of the cerebellum. The fibres from the cerebral cortex form synapses with the cells in the pons whose axons proceed to the opposite cerebellar surface. We thus have disclosed a mechanism by which impulses or influences leaving one region or another of the cortex of one cerebral hemisphere may, by a relay in the pons, be brought to bear on the superficial grey matter of the cerebellum of the opposite side. At the same time it is possible that some of the fibres in question supply a mechanism working in an opposite direction. It may be that some of the fibres of the middle peduncle are axons of Purkinjé cells which carry impulses from the cerebellar surface to the pons of the opposite side, and these, by a relay, start other impulses passing up to the cerebral cortex on the same side so far as the pons is concerned, but opposite so far as the cerebellum is concerned. This however remains to be more definitely determined by future enquiry. We may add that a similar question arises with regard to the inferior peduncle. The dominant fibres of this are fibres carrying impulses to the superficial grey matter of the cerebellum, especially perhaps to that of the median vermis, but whether there are not also fibres carrying impulses from the cerebellum to the bulb and spinal cord is a matter on which observers are not agreed.

The superior peduncle is obviously of a more mixed nature. We have seen that as it leaves the cerebellum it is joined by fibres from the antero-lateral ascending tract of the cord of the same side, which run back along it presumably to the superficial grey matter. The peduncle itself, running forwards and decussating ventral to the corpora quadrigemina, may be traced to the red nucleus of the opposite side. According to most observers the decussation is complete; but it is stated that some fibres coming from the opposite side of the cerebellum do not decussate. The whole peduncle does not actually end in the nucleus. Some of these fibres simply pass through the nucleus, and end elsewhere. Without going into details it may be said that either indirectly through the red nucleus or other structures belonging to, or connected with, the tegmentum, or directly by fibres passing up to the cortex, the superior peduncle furnishes a connection between one side of the cerebellum and the cortex of the opposite hemisphere; and indeed it used to be called the 'processus a cerebello ad cerebrum.'

We further have reason to believe that this connection is a double one, in the sense that it consists on the one hand of fibres carrying impulses from the cerebral hemisphere to the cerebellum, and on the other of fibres carrying impulses in the opposite direction. From cells in the red nucleus axons may be traced into the peduncle; these supply a path for impulses to the cerebellum. As we have seen, this superior peduncle is largely connected with the nucleus dentatus, and the axons in question may end in the grey matter of that nucleus; but if so, the cells of the nucleus serve simply as a relay, the impulses passing on from the nucleus to the superficial grey matter. Some of the fibres of the peduncle, however, appear to pass directly to the grey matter, without any relay. Conversely, impulses leaving the cerebellar superficial grey matter along the axons of cells of Purkinjé appear to pass into the peduncle, either directly or indirectly through a relay in the nucleus dentatus.

Thus, though many details have to be settled by future inquiry, we have evidence that the superficial grey matter of the cerebellum of each side is connected on the one hand chiefly by the inferior peduncle with the sensory machinery of the body at large of the same side, including the special afferent mechanism of the vestibular nerve, and, on the other hand, by the other peduncles with the cerebral cortex of the opposite side.

The anatomical arrangement suggests that in carrying out some at least of the work which sensory impulses have to do, the cerebellum and the cerebral cortex act together, the one-half of the cerebellum acting with the opposite cerebral hemisphere.

In that part of the work of sensory impulses which culminates in psychical labours, in sensations properly so called, in perceptions and the like, the cerebellum appears to have nothing whatever to do. It appears to be concerned only with sensory afferent impulses in so far as these enter into the development of movements carried out by the skeletal muscles. And even in respect to these its action is limited. No kind of movement is missing as the result of cerebellar failure, as is the case when the pyramidal tract or the sensory path itself is interfered with. An animal in the absence of the cerebellar machinery can execute all its ordinary movements. What is lacking is precision and completeness in the movements.

We are thus led to suppose that when a movement is about to be carried out, the sensory impulses whose existence, as we have seen, is essential to the completion of any movement due to the action of the central nervous system, stream up to the cerebellum and to the cerebral cortex at the same time, the impulses from one side of the body going to the cerebellum of the same side and to the cerebral cortex of the opposite side. We are further led to suppose that then something passes between the cerebellum and the cerebral cortex, by means of which the efferent impulses which appear as the outcome of the whole nervous act pass down to their appropriate destinations in an efficient manner.

Much more than this we are not at present in a position to say. Some of the facts seem to point to the cerebellum exerting a moderating, restraining influence on the cortex. Thus the deviation of the eyes observed after removal of half the cerebellum seems to be due to an over-action of the opposite cerebral hemisphere; and, as we have said, other indications of unilateral over-action have been noticed. Moreover it is stated that after removal of half the cerebellum, the excitability towards artificial stimulation of the Rolandic cortex of the opposite cerebral hemisphere is exaggerated. But it would not be profitable to dwell on this matter at length. Nor, even admitting such a view, can we state with certainty what are the channels by which the cerebellum acts on the cerebral cortex. As we have seen, both the middle and superior peduncle seem to furnish a path for impulses from the cerebellum to the cerebrum; but the path from the cerebrum to the cerebellum seems a much more prominent one, though it is the former path which, according to our ordinary conceptions, is postulated by the view in question. We say, according to our ordinary conceptions, but as we have already more than once insisted, we must not assume that within the central nervous system at all events, an axon carries impulses exclusively from the perikaryon towards its own terminals. It may be that the play between cerebrum and cerebral is of a kind which cannot be denoted by such terms as centrifugal and centripetal.

The great complexity in the structure of the superficial grey matter of the cerebellum justifies us in assuming that much nervous 'business' is carried on there. That business, whatever it may be, never, so far as we know, crosses the threshold of consciousness, however near it may come to it; it seems to be, in some way or other, occupied simply with the due carrying out of muscular contractions, and the fact that so intricate and manifold a nervous machinery seems necessary for, so to speak, the mere superintendence, of bodily movements, may be taken as a warning of how little after all we know of the real inner working of the brain.

§ **688**. Concerning the functions of the rest of the brain lying between the spinal cord and the cerebral cortex, unless we were to enter into details which would be unfitting here, very little remains to be said beyond what has already been said in the previous discussions. With regard to all this part of the brain, the results of experimental interference are uncertain and of little value unless they are distinctly corroborated by anatomical teachings, and the same perhaps may be said even of clinical observations. Our anatomical knowledge, though rapidly increasing, still leaves much to be desired; and we must for the present be content with conceptions which, in the absence of an adequate anatomical basis, must necessarily be general and vague.

Many of the constituents of the bulb and of the tegmental region, the nuclei of the cranial nerves, and the structures immediately connected with these, such for instance as the posterior longitudinal bundles, may be regarded as analogues, though perhaps more elaborately developed, of spinal nervous mechanisms, mechanisms of an afferent or of an efferent nature, or mechanisms bringing these two into direct relation; they may be looked upon as corresponding in a broad way to the simple spinal mechanisms engaged in carrying out ordinary reflex actions.

Other parts of the region in question may be regarded as mechanisms for the special senses, mechanisms of the same class as the above but much more highly developed. As we have seen, the anterior corpora quadrigemina form in part at least a visual mechanism. In the lower animals, as we have said, these bodies probably carry out a great deal of the whole business of 'sight'; in the higher animals their work seems largely restricted to bringing visual impulses into direct relation with the motor nervous mechanisms of vision. Injury to, or removal of, or disease of these bodies interferes with sight, the exact mode in which vision is thereby affected differing in different kinds of animals; and artificial stimulation of them, as by electrical currents, calls forth among other things movements connected with vision. The posterior corpora quadrigemina seem, as we have also seen, in a somewhat similar way connected with hearing. In view of what was said above as to so many of these cerebral structures being mechanisms, either simple or elaborate for bringing afferent impulses into connection with appropriate motor mechanisms, it may be interesting to note that stimulation of the surface of the posterior corpora quadrigemina, in the monkey and some other animals, among other effects gives rise to a peculiar cry or bark; it is stated moreover that removal of these bodies not only renders the animal more or less deaf but also interferes with or in some way changes the voice. In the frog, too, the optic lobes, a part of which corresponds to the posterior corpora quadrigemina of the mammal, contain the nervous mechanism for the croaking mentioned in § 638; when these are removed that kind of croaking cannot be brought about. This part of the brain seems to supply a mechanism by which the nervous impulses, giving rise to vocal movements, are brought into relation with auditory impulses.

All the parts of the brain which we are now considering, namely, those from the optic thalamus backwards, are developed out of the primitive brain, ending in front in the third ventricle, the cerebral and olfactory vesicles being subsequently added. In the lower animals, for instance in the fish, these parts are the instruments of so much of the nervous life of these animals, and even of such psychical life as they possess, that the loss of nervous functions, which is entailed by the loss of the cerebral hemispheres, is with difficulty appreciated. The fish deprived of its cerebral hemispheres is not only able to carry out all its ordinary movements apparently as well as before, but moves of its own accord, retains what we call its 'will.' As we ascend the animal scale, the whole of this part of the brain is made, as we have attempted to shew in preceding sections, increasingly subservient to the behests of the cerebral cortex, until in man it seems to be reduced to little more than a nervous machinery, whose action we designate by the vague term of 'coordination of movements.' That coordination entails, in many cases at least, a considerable development of afferent impulses; these, through the agency of this central machinery acquire, as we were led to believe in treating of vision, characters different from those which they possess as they are sweeping along the peripheral afferent fibres, and are thereby at the same time fitted for the further use of them by the cerebral hemisphere; but we are not at present in a position to state what is the nature of that development or to explain how coordination is effected, or indeed what we exactly mean by it. The little we have been able to say about the cerebellum leads us to believe that the part played by that organ in coordination has to do on the one hand with the general afferent impulses concerned in the movements of the skeletal muscles, namely, those from the skin, muscles, joints and tendons, and on the other hand with the special vestibular impulses. At the same time that little shews us how complicated in this respect is the action of the cerebellum, and warns us not to carry too far into the interpretation of what it does, the conceptions of nervous impulses which we have gained from the behaviour of peripheral afferent or efferent fibres under artificial treatment; the mere passage this way or that of ordinary impulses, whether sensory or motor, seems insufficient to explain cerebellar action. We may bear this warning in mind when we are dealing with matters about which we know even less than about the cerebellum, with the work of the anterior corpora quadrigemina in weaving visual impulses, and with that of the posterior corpora quadrigemina in weaving auditory impulses into the 'coordination' web.

These two bodies seem further to have 'coordinating' work to do, other than that connected with either sight or hearing, and yet different from that of the cerebellum. In the lower animals, as in the frog, the optic lobes, not yet differentiated into the above two bodies, seem to have a special connection with coordination; a frog deprived of its optic lobes loses the power of balancing, which it retains (§ 638) after the removal of the hemispheres. But what in the mammal such a work of the two bodies is we can not at present tell. Still less perhaps can we say anything definite beyond what has been said in preceding pages about the optic thalami or the sub-thalamic and other structures which are clustered round the end of the third ventricle.

§ **689**. Besides the somatic functions which in previous discussions we have chiefly had in view, the brain as a whole undoubtedly carries out splanchnic functions; concerning these, however, we must be very brief.

Of the respiratory and vaso-motor functions of the bulb we have already treated in their appropriate places, and we have referred (§ 535) to the experimental evidence that a lesion of the corpus striatum, or of the front part of the optic thalamus has a remarkable influence on the development of heat in the body. We have further seen that the higher parts of the brain, acting through the bulb, exercise powerful influences on respiration, on the vaso-motor system, and on the beat of the heart. Daily experience affords abundant instances of actions such as these, as well as of the influence of the brain on other organic functions. We can bring our will to bear on the mechanism of micturition (§ 430) which is almost wholly, and on the mechanism of defæcation (§ 275) which is largely, splanchnic in nature. These movements, however, are not skilled movements; and as we explained in dealing with them, the action of the brain as regards them seems limited to augmenting or inhibiting the activity of spinal centres. We should therefore hardly expect them to be specially represented in the cortex. But emotions have a much wider and more powerful influence over the splanchnic functions than has the will, and have the power of affecting the work of certain organs, for instance the heart and secreting glands, which the will is unable to touch. And since we have reason to believe that the cortex is closely associated with the emotions, we may naturally infer that elements of the cortex supply a link in the chain through which an emotion influences this or that splanchnic activity; we may, accordingly, expect to find that stimulation of some part or other of the cortex produces splanchnic effects. The results of experimental investigation, however, are both scanty and discordant. Thus, some observers find that the stimulation of the cortex, the locality being in the dog some part of the sigmoid gyrus, produces movements of the bladder; and they trace the path of this influence through the front part of the thalamus and the tegmentum to the bulb, and so to the cord, excluding the cerebellum, which other observers believed to be concerned in the matter. So also stimulation of the cortex may produce a flow of saliva; and stimulation of some part or other of the Rolandic area produces a flow more readily than does stimulation of other parts of the cortex. But the results of experiments do not agree in indicating a definite localisation like that for movements; and indeed it may be argued that the secretion, when it does occur, is an indirect and not a direct effect of the cortical stimulation. It is perhaps worthy of note that no one has observed stimulation of the cortex to produce pilo-motor effects (§ 437), though erection of the hairs is a conspicuous emotional sign.

Similarly, stimulation of parts of the cortex has in the hands of various observers led to movements or to arrest of movements of the intestines, to changes in the beat of the heart, and to various vaso-motor and other effects; but it will not be profitable to enter into any further details. We may, however, add the remark that when the cortical motor area for a limb is removed, or suffers a lesion, the temporary paralysis which is thereby caused is accompanied by a rise of temperature in the limb; this may be at times very great indeed; in the monkey, for instance, the hand or foot on the paralysed side may be as much as 5° C. higher than that of the other side. The effect is partly due to vaso-motor paralysis, but, especially considering that the muscles of the limb are relatively quiescent and so producing less heat than usual, cannot be due to that alone. The remarkable result may be taken as still further illustrating the complexity of the processes connected with the cortical Rolandic area; this area seems in some way associated with the vascular arrangements and nutrition of the muscles with whose movements it is concerned.

In this connection it may be worth while to call attention to the striking change which takes place in the general metabolism of such an animal as a dog, when the cerebral hemispheres are removed or curtailed. In the case of the dogs referred to in § 641, from which nearly the whole of both hemispheres had been removed piecemeal, the daily meal had to be largely, one might almost say enormously, increased, in order to keep the animal in health or even alive; in fact a great increase in bodily metabolism seemed to be as notable or even a more notable effect of the loss of the cerebral cortex than the modifications of sensation or movement which were observed. The histories of these dogs leave on the reader the impression that the great use of the cerebral cortex is to regulate the nutrition of the body; and although we may probably assume that the effect is brought about in some indirect manner, still the mere fact illustrates very forcibly the complexity of the work of the brain.

§ **690**. There remain yet a few more words to be said about the cerebral cortex. We regard, and justly so, the spontaneous intrinsic activity of the brain as the most striking feature of its life. The nearest approach to it which we find elsewhere in the body, is perhaps the rhythmic beat of the heart. The analogy between the "regular automatism" of the one and the "irregular automatism" of the other is a striking one; and indeed our knowledge of the relatively simple spontaneity of the heart has probably influenced to a large extent our conceptions of the complex spontaneity of the brain. In the heart the rhythmic discharge of energy is chiefly determined by intrinsic chemical changes, by the metabolism of the cardiac substance; the influence of external circumstances, apart from those which provide an adequate supply of proper blood, is wholly subsidiary and serves only to raise or to lower the intrinsic changes from time to time, as occasion may demand. And the analogy of the heart has perhaps led us to exaggerate the part played in the brain by the like intrinsic chemical metabolism. (We are here of course viewing the action of the brain from the only stand-point admissible in these pages, the purely physiological one; but such a mode of treatment does not prejudge other points of view.) Some writers use expressions which seem to imply the conception that the nervous changes forming the basis of the psychical and other processes of the brain are chiefly the direct outcome of the chemical metabolism of the grey matter, and especially of the nerve cells. They speak of "the discharge of energy" from these cells in the same way that we can speak of the discharge of energy from a cardiac fibre. But, to say nothing of the low rate of nervous metabolism as measured in terms of chemical energy, we have no experimental or other evidence of nervous substance in any part of the body being, like the cardiac substance, the seat of an important metabolism carried on independent of influences other than purely nutritive ones. In the case of nerve cells interpolated along nerves composed of fibres of the same kind, as in the sporadic ganglia, all the instances where the nerve cells were supposed to initiate active processes have, on examination, broken down; as we have seen, the ganglia of the heart do not supply the moving cause of the heart beat. It is only in the central nervous system, the dominant character of the grey matter of which is the multiple junction of nerve cells having different connections, the junctions being thickest and the cells most varied where the work is highest, that we have any evidence of "discharge of energy" from the cells.

As we pointed out (§ 597) in speaking of the spinal cord, the discharge of efferent impulses from the central nervous system, though it undoubtedly must have a certain chemical basis, namely, the metabolism of the nervous substance, is, in the first line, dependent on the advent of afferent impulses. But this, if true of the spinal cord, is still more true of the brain, which receives or may receive not only all the impulses which reach it through the cord, but especially potent and varied impulses directly through the cranial nerves. All life long the never-ceasing changes of the external world continually break as waves on the peripheral endings of the afferent nerves, all life long nervous impulses, now more, now fewer, are continually sweeping inwards towards the centre; and the nervous metabolism, which is the basis of nervous action, must be at least as largely dependent on these influences from without, as on the mere chemical supply furnished by the blood from within.

We have developed this point because of the influence it must have on our conceptions of the physiological processes taking place in the cortex. If we accept the view just laid down, we must regard the supereminent activity of the cortex and the characters of the processes taking place in it as due not so much to the intrinsic chemical nature of the nervous substance which is built up into the cortical grey matter as to the fact that impulses are continually streaming into it from all parts of the body, that almost all influences brought to bear on the body make themselves felt by it. To put the matter in a bald way we may ask the question, what would happen in the cortex if, its ordinary nutritive supply remaining as before, it were cut adrift from afferent impulses of all kinds? We can hardly doubt but that volitional and other psychical processes would soon come to a standstill and consciousness vanish. This is indeed roughly indicated by the remarkable case of a patient, whose almost only communication with the external world was by means of one eye, he being blind of the other eye, deaf of both ears, and suffering from general anæsthesia. Whenever the sound eye was closed, he went to sleep. It is further indirectly illustrated by the following experimental result. We have seen (§ 654) that a vertical incision carried through the depth of the grey matter around an area does not prevent stimulation of the surface of the area producing the usual movements. But after such an incision the animal suffers a paralysis of the movements connected with the area, like that resulting from the removal of the grey matter of the area; and the operation is said to be followed by degenerative changes in the area, and degeneration of the pyramidal fibres starting from it. Some of this effect may be due to nutritive changes brought about by injury to the pia mater and division of blood vessels; but it cannot be wholly accounted for in this way; it appears as if the life of the area is curtailed when its nervous ties are broken. We may conclude then that we are not justified in speaking of consciousness or volition, or other psychical processes, even admitting that these fail when the cortex is removed, as being functions of the cortex in the same way that we speak of the functions of other organs; they are rather functions of the connections of the cortex with the other parts of the central nervous system.

The higher psychical processes we may probably regard as being preeminently functions of the connections of the several parts of the cortex with each other. We have seen that we may roughly classify the fibres of the cortex into 'projection fibres,' connecting the cortex with lower parts, either, like those of the pyramidal tract, centrifugal, carrying impulses from the cortex to lower parts, or, like those of the optic radiations, centripetal, carrying impulses from the lower parts to the cortex, into 'commissural' (which are chiefly 'callosal') fibres, connecting the cortex of one hemisphere with that of the other hemisphere, and into 'association' fibres, connecting one part of the cortex with other parts of the cortex of the same hemisphere. In the preceding discussions we have had to do mainly with projection fibres. Concerning the 'commissural' fibres very little definite can be said. We may assume in a general way that it is mainly through these that, though we possess two hemispheres, we seem to have 'one mind'; but the whole of the matter is obscure. We do not at present know what is the exact range of correspondence in function between the two hemispheres, whether for instance for the unilateral feature of speech (§ 659) is quite exceptional, or where it is merely one example among many. Even if we suppose that a spot on one hemisphere corresponds as a rule physiologically, that is in function, with the spot on the other hemisphere, which is its anatomical fellow, we find that the callosal fibres from the one spot are not exclusively or even chiefly distributed to the fellow spot. Nor can we at present clearly explain why certain areas of the cortex, as for instance that of the island of Reil, possess few commissural or at least callosal fibres. And even when we have assigned to these commissural fibres their fullest value, they do not really help, as we saw in treating of visual sensations, us to understand how two sensory impulses from the two sides of the body produce one affection of consciousness.

When we turn to 'association fibres' we seem able to see our way a little further. The Rolandic area is more richly provided with projection fibres, partly centrifugal, partly centripetal, than any other part of the cortex; but in the higher monkeys and by inference still more so in man, the foci in this area, stimulation of which gives rise to movements, are separated by inexcitable cortex. From these inexcitable patches no pyramidal fibres start, and we may infer that they are at the same time free from fibres carrying centripetally impulses from lower parts, so closely bound together, as we have seen, are the ingoing sensory and the outgoing motor impulses. Hence, even in the Rolandic area, there are many, not only cells but groups of cells, which have no line of communication of their own with the periphery of the body of the individual to which they belong, and so with the outside world; their functional life is dependent on 'association' fibres (we may for clearness' sake omit the commissural fibres) which keep them in touch with cells having such lines of communication. Even the scanty description which we gave some time ago of the minute structure of the cortex will suffice to shew how such 'associations' can be carried out. In the temporo-occipital region, even making every allowance for the optic radiations and the corresponding auditory fibres, as well as for the visual auditory or motor centrifugal fibres and for the cortici-pontine fibres passing from the cortex through the pes to the pons (§ 632), by which cells in this region are in touch with the lower structures, there must be a vast number of cells whose functional life is also dependent on association fibres. And if we turn to the inexcitable frontal region in front of the Rolandic region, making every allowance for the cells connected by the cortici-pontine fibres through the pes with the pons, and for the cells of the dwindled olfactory mechanism, we find here again a multitude of such cells.

In fact by far the greater number of the cells which make up the complex 'tangle' of the cortex, probably more than half of them are cells whose whole life, putting aside the influences of the mere raw material brought to them by the blood, is dependent on association fibres connecting them with other cortical cells. These are cells which receive directly none of the impulses sweeping up to the cortex through the thalamus and other tegmental structures from the sensory nerves of the body, which emit directly no motor impulses through the pyramidal tract or other tracts to the muscles or other structures. A sensory impulse, or perhaps to be more exact, we ought to say, the outcome of a sensory impulse can only reach them through an association fibre from some other cell in the cortex; they can give rise to an outward token of their activity, only by acting through an association fibre on some other cortical cell which, unlike itself, has connections with lower parts of the nervous system.

Such cells, we may safely assume act, by virtue of their manifold connections, as the main agents of psychical processes. We are not at present able, in respect for instance to a cortical cell with which a fibre of the optic radiations effects a synapsis, to define exactly what is going on in the cell when an impulse, or whatever we may please to call it, reaches the cell along the fibre. We cannot at present give the events a name. But we may be sure that what takes place does not constitute full psychical vision, the whole of the psychical effects of the impulse; these are completed by means of cells connected with the former by association fibres. And so in other cases.

This view of the psychical qualities of association fibres and their belonging cells is supported by histological evidence of a special kind. We have reason to believe that the myelination of a nerve fibre is one of the conditions of its functional completeness, and we have seen that this takes place at different times in different parts of the nervous system during the development of an individual. It takes place moreover in such a way as to justify the view that the later the myelination of a fibre, the higher the function of the mechanism of which that fibre is a part. Now not only do the fibres of the cerebral cortex myelinate later than those of other parts, but the association fibres myelinate much later than the projection fibres; in some cases the myelination of these does not take place until adult life. Further, when as often occurs, the association fibre is the collateral of a projection fibre, the myelination of the collateral may be deferred until a long time after the main axon has acquired its medulla. This may be taken to mean that the main axon of fibre in question has for a long time been able to carry out its own work, for instance, its share in a voluntary movement before that work is accompanied by the psychical events which ultimately do accompany it; if the fibre were a centripetal fibre, one for instance of the optic radiations, we may suppose that long after the power of receiving visual sensations had been gained, the power of retaining the sensation in memory, or of working it up into an idea, had not yet been acquired.

As we have seen, we have increasing evidence of a localisation of function in the cerebral cortex in the sense that certain regions of the surface are especially related to parts of the body, the retina to the occipital cortex, the hand to a portion of the Rolandic area and so on. We have evidence of a like localisation in respect to psychical events, a localisation also having relation to parts of the body. Thus, as we have seen, a particular area of the cortex has to do with the psychical processes intervening between vision and speech, or between hearing and speech, as shewn in word blindness and word deafness (§ 661 and § 677); the entire 'projection' mechanism for vision and that for speech in such cases may be intact, the individual can see, or can hear, and can speak; but the association mechanism connecting the shewn or the heard word and the speaking of it, and this alone, has broken down. Such cases are probably instances of a localisation of psychical processes obtaining largely in the cortex.

Whether there be another kind of localisation having reference to the essential nature of the psychical processes, irrespective of the parts of the body, and of the particular nerves whose excitation may be the starting point of the psychical processes, whether for instance, to put the matter baldly, a particular part of the cortex is especially concerned with the 'emotions' and another with the 'intellect' is a wholly different question. To deal with this we have little or no precise knowledge as a guide. It is true that many observers report as a striking effect of removal of, or interference with, the frontal lobes, in the dog and in the monkey, an alteration in the personal characteristics of the individual; the mild and inoffensive become morose and vicious, the shy and retiring become demonstrative and 'gushing.' Again, the brains of men of great 'intellectual power' are often, or at least sometimes, especially highly developed in the temporo-occipital region. And so on. All this, however, stands on a very different footing from the more exact knowledge rapidly increasing, which, as shewn in preceding sections we now possess, concerning the nature of that which is done by the projection mechanisms; and it is probably working up from these that we shall gain light as to the psychical events of which the projection events are after all the basis. Even the higher psychical events cannot truly be spoken of as functions of the cortex, in the sense that they are simply the outcome of molecular changes in the cortical grey matter; they are rather to be regarded as the outcome of complex processes in which the parts of the brain below the cortex play a part no less essential than that of the cortex itself. The fibres passing down from the cortex to the middle brain have probably functions by which they take part even in our psychical life, functions for which neither the words motor nor sensory are fitting.

SEC. 11. ON THE TIME TAKEN UP BY CEREBRAL OPERATIONS.

§ **691.** We have already seen (§ 594) that a considerable time is taken up in a purely reflex act, such as that of winking, though this is perhaps the most rapid form of reflex movement. When the movement which is executed in response to a stimulus involves cerebral operations a still longer time is needed; and the interval between the application of the stimulus and the commencement of the muscular contraction varies according to the nature of the mental labour involved.

The simplest case is that in which a person makes a signal immediately that he perceives a stimulus, *ex. gr.* closes or opens a galvanic circuit the moment that he feels an induction shock applied to the skin, or sees a flash of light, or hears a sound. By arrangements similar to those employed in measuring the velocity of nervous impulses, the moment of the application of the stimulus and the moment of the making of the signal are both recorded on the same travelling surface, and the interval between them is carefully measured. This interval, which has been called 'the reaction period' or 'reaction time,' may be divided into three stages: (1) The time during which afferent impulses are generated in the peripheral sense organs and transmitted along the afferent nerves to the central nervous system; this may be called the "afferent stage." (2) The time during which, through the operations of the central nervous system, the afferent impulses are transformed into efferent impulses; this may be called the "central stage." (3) The time taken up by the passage of the efferent impulses along the efferent nerves and the transformation of the nervous impulses into muscular contractions; this may be called the "efferent stage." In the efferent stage the events are comparatively simple, and though not absolutely constant, do not vary largely; we are able to form a fairly satisfactory estimate of its duration and so of the share in the whole reaction period which may be allotted to it. The events of the afferent stage are much more complex, and the estimates of its duration, being arrived at in an indirect manner, and chiefly based upon calculations of the whole reaction time, are very uncertain. The fact that the reaction time with cutaneous stimulation is shorter when the stimulus is applied to the hand than when it is applied to the arm, though in the latter case the tract for simple afferent impulses is longer, illustrates the complexity of the matter; the reaction time is shorter with the hand because the hand is more distinctly a sensory organ. Hence all attempts to estimate the length of the "central" stage, the "reduced reaction period" as it is sometimes called, by subtracting the efferent and afferent stages, must be subject to much error. But a good deal may be learnt by studying the variations under different circumstances of the reaction period as a whole.

Taking first of all the cases in which the events of the central stage are simple, such as those where the subject has merely to make a signal upon feeling a sensation, we find that the length of the reaction period is dependent on the intensity of the stimulus, being shorter with the stronger stimulus. But variations in the strength of the stimulus, especially in the case of minimal stimuli, have a much more striking effect in determining the certainty of the reaction than in affecting the length of the period. Thus when the signal is made in response to some visual sensation, upon seeing an electric spark for instance, if the spark be a very weak one the subject of the experiment often fails to make the signal at all, though he may rarely fail if the spark be a strong one.

Some of the most marked variations in the length of the reaction period are determined by the individuality of the subject. Thus with the same stimulus applied under the same circumstances the reaction period of one person will be found very different from that of another.

The length of the reaction period varies also according to the nature and disposition of the peripheral organs stimulated. In general it may be said that cutaneous sensations produced by the stimulus of an electric shock applied to the skin (the signal for instance being made by the right hand when the shock is felt by the left hand) are followed by a shorter reaction period than are auditory sensations, while the period of these is in turn shorter than that of visual sensations produced by luminous objects; on the other hand, the shortest period of all is said to be that of visual sensations produced by direct electrical stimulation of the retina. Roughly speaking we may say that the reaction period is for cutaneous sensations $\frac{1}{7}$th, for hearing $\frac{1}{6}$th, and for sight $\frac{1}{5}$th of a second. But individuals differ much in the relative reaction period for the several kinds of sensation; and these figures are given as illustrations merely, not as having absolute worth.

Practice materially shortens the reaction period; indeed, after long practice, making the signal, at first a distinct effort of the will, takes on the characters of a reflex act, with a correspondingly shortened interval. Lastly, we may add that in the same individual and with the same stimulus, the length of the period will vary according to circumstances, such as the time of year, the weather, and the like, as well as according to the condition of the individual, whether fresh or fatigued, fasting or replete, having taken more or less alcohol, and the like.

The reaction period of vision has long been known to astronomers. It was early found that when two observers were watching the appearance of the same star, a considerable discrepancy existed between their respective reaction periods, and that the difference, forming the basis of the so-called 'personal equation,' varied from time to time according to the personal conditions of the observers.

§ **692**. The events taking place in the central stage are of course complex, and this stage may be subdivided into several stages. Without attempting to enter into psychological questions, we may at least recognize certain elementary distinctions. The afferent impulses started by the stimulus, whatever be their nature, when they reach the central nervous system undergo changes, and as we have seen, probably complex changes, before they become sensations; and further changes, now of a more distinctly psychical character, are necessary before the mind can duly appreciate the characters of these sensations and act accordingly. Then come the psychical processes through which these appreciated sensations, or perceptions, or apperceptions as they are sometimes called, determine an act of volition. Lastly, there are the executive processes of volition, the processes which, psychical to begin with, end in the issue of coordinate motor impulses, or, in other words, start the distinctly physiological processes of the efferent stage. We may thus speak of the time required for the perception of the stimulation, of the time required for the action of the will, and of the time required for the complex psychical processes which link these two together. Accepting this elementary analysis, it is obvious that the total length of the central stage may be varied by differences in the length of each of these parts; and a more complete analysis would of course open the way for further distinctions. Hence, by studying the variations of the whole reaction time under varying forms of psychical activity, we may form an estimate of time taken up by various psychical processes.

We may take as an instance the case in which the subject of the experiment has to exercise discrimination. The mode of making the signal being the same, and the stimulus being of the same order in each trial, that is to say, visual, or cutaneous, or auditory, &c., and general circumstances remaining the same, two different stimuli are employed, and the subject is required to make a signal in response to the one stimulus, but not to the other; the subject has to discriminate between the psychical effects of the two stimuli. Suppose, for example, the stimulus is the sound of a spoken or sung vowel, and the subject is required to make a signal when *a* is spoken or sung, but not when *o* is spoken or sung. If the subject's whole reaction period be determined (i) in the usual way, with either *a* or *o* spoken (and the result will be found not to differ materially whether *a* or *o* be used), the subject knowing that only *a* or only *o* will be spoken, and then be determined again (ii) when he has to discriminate in order that he may make the signal when *a* is spoken but not when *o* is spoken, he not knowing which is about to be spoken, the whole reaction period will be found to be distinctly longer in the second case. The experiment may be varied by making use of all the vowel sounds taken irregularly as the stimulus, the subject responding by a signal to one only, as arranged beforehand. And of course other orders of stimulus may be used, either visual, the signal being made when a red light is shewn but not when other colours are shewn, or tactile, the signal being made when one part of the body is touched but not when other parts are touched, and the like.

In such experiments where the subject has to distinguish, to discriminate between two or more events, the prolongation of the reaction period is obviously due to the longer time required for the psychical processes taking place during what we have called the central stage. In the two cases, one without and the other with discrimination, not only are the afferent and efferent stages the same in both, but we have no reason to suppose that in the central stage is there any difference between the two cases as to the time taken up by the transformation of simple sensory impulses into perceptions, or as to that taken up by the will in gaining access to the motor apparatus and so starting the processes of the efferent stage; the delay takes place in the psychical processes intervening between these two parts, and the amount of delay is the measure of the time needed for the processes involved in the discrimination. This "discrimination period" has been found to differ in the same individual according to the sensation employed, visual, auditory, &c., and according to the kind of difference in the sensation which has to be discriminated, for instance in visual sensations between colours or between objects in different parts of the field of vision. In a series of observations made in this way, the discrimination period, *i.e.* the prolongation of the simple reaction period due to having to discriminate, was found to range from 0·011 sec. to 0·062 sec.; but these figures also are given rather as an illustration than for their absolute worth.

Another series of observations may be made in the following way. The signal being one made with the hand, the simple reaction period for a stimulus is determined with the signal given by the right hand. Two kinds of stimuli are then employed, both of the same order, two vowel sounds for instance, and the subject is directed to respond to one vowel with the right hand and to the other with the left hand. It is found, the subject being right-handed, that the reaction period is greater when the signal is made with the left hand. In this case the delay takes place not in the recognition of the effects of the stimulus, nor in the processes through which the will is formed upon that recognition; these are the same in the two cases; it takes place in the processes by which the will is brought to bear on the nervous motor apparatus for making the signal, on the cortical origin, for example of the pyramidal tract; these processes take a longer time in the case of the unaccustomed left hand than in the case of the usual right hand. In this way we obtain a measure of so to speak the volitional side of psychical processes.

In a somewhat similar way we may obtain a measure of the time required for perception. A strong sensation following too closely upon a weak one will prevent the psychical recognition of the weaker one. If, for instance, two or three letters in white on a black background be presented to the eye, and a large white surface be presented afterwards at an interval which is made successively shorter and shorter, it is found that when the interval is made very brief indeed the letters cannot be perceived at all. In proportion as the interval is prolonged, the recognition of the letters increases, until at an interval of about ·05 sec. they are fully and clearly recognized. That is to say, the time required for perception is in such a case of about that length.

The duration of all these psychical processes, as of the simple reaction period itself, varies of course under different circumstances, and the discrimination period may be conveniently used for measurements of the varying effects of circumstances. Practice shortens the discrimination period as it does the simple reaction period. One of the most powerful influences is that of attention. And it is stated that the shortening of the period is greater when the attention is concentrated on the making of the signal than when it is more especially directed to recognition of the stimulus; in other words, the volitional processes are more amenable than are the perceptive processes to the psychical action which we call attention. On the other hand, the period is distinctly prolonged if the observer be distracted by concomitant sensations. For example, the period for discriminating between two visual sensations is prolonged if powerful auditory sensations be excited at the same time.

The same method of measurement may be used in other ways and under other circumstances with reference to psychical processes. It must be remembered, however, that all such observations are open to many fallacies and need particular caution. It not unfrequently happens that false results are obtained; for instance, the subject, expecting the stimulus to be brought to bear upon him and straining his attention, makes the signal before the stimulus actually comes off. And the interpretation of the results obtained are in many cases very difficult; but it would be out of place to dwell upon these matters any further here.

SEC. 12. THE LYMPHATIC ARRANGEMENTS OF THE BRAIN AND SPINAL CORD.

§ **693**. *The Membranes of the Brain and Spinal Cord.* The cerebro-spinal canal is lined by a tough lamellated membrane, composed of connective tissue with a small amount of elastic networks, called the *dura mater*, which, somewhat closely adherent to the walls of the cranial cavity, is separated from those of the vertebral canal by a considerable space, containing blood vessels, especially large venous sinuses, and some fat. It may be considered as a development of the periosteum lining the cerebro-spinal cavity. It sends tubular sheaths for some distance along the several cranial and spinal nerves; and forms between the cerebral hemispheres, in the longitudinal fissure, a conspicuous sickle-shaped vertical fold, the *falx cerebri*, as well as a smaller horizontal or oblique fold between the cerebellum and cerebrum known as the *tentorium*.

The vascular *pia mater* is closely attached to the surface of the brain and spinal cord, dipping down as we have seen into the ventral or anterior fissure of the cord as well as into the fissures of the brain. Sheath-like investments of pia mater are continued along the several nerves as they leave the cerebro-spinal cavity; and in the vertebral canal an imperfect partition half-way between the dorsal and ventral surfaces of the cord is furnished by a membrane of connective tissue which, continuous along its whole length with the pia mater, is attached to and fused with the dura mater at intervals only, namely, between the successive nerve roots. Since its outer edge has thus a toothed appearance, this membrane is called the *ligamentum denticulatum*. Between the pia mater next to the brain and cord and the dura mater next to the bony walls is a cavity, which is divided into two by a thin membrane, *the arachnoid*, composed of interwoven bundles of connective tissue. The space between the arachnoid and the dura mater is called the *subdural space*, and the space between the arachnoid and the pia mater is called the *subarachnoid space*.

When the brain is exposed by removing the roof of the skull and slitting open the dura mater, the subdural space is laid bare, and the arachnoid is seen stretching over the pia mater; in the vertebral canal the arachnoid lies close to the dura mater, so that usually, when the dura mater is slit open and turned back, the arachnoid is carried with it and the cavity exposed is that of the subarachnoid space. The arachnoid, like the dura mater and the pia mater, is continued for some distance over the nerves as they leave the cerebro-spinal cavity; so that each nerve at its exit is surrounded by a tubular prolongation of the subdural space, and within this a similar tubular prolongation of the subarachnoid space.

The subdural space is broken up to a slight extent only by bridles carrying nerves and blood vessels, especially venous sinuses, between the pia mater and dura mater, and, over the surface of the brain, by villus-like projections of the arachnoid, called Pacchionian glands, some of which pierce the venous sinuses of the dura mater. It is lined throughout, both on its dural and on its arachnoid wall, by an epithelium of flat epithelioid cells, and may be compared to a serous cavity such as that of the peritoneum. Like the serous cavities it contains normally a small quantity only of fluid, and its size is potential rather than actual.

The subarachnoid space on the other hand is, especially in certain regions, such as the dorsal portions of the vertebral canal and the base of the brain, much broken up by bridles of connective tissue passing from it to the pia mater, as well as by a network or sponge-like arrangement of bundles of connective tissue lying immediately beneath itself, and giving it when viewed from below a honeycomb or fenestrated appearance. The under surface of the membrane itself as well as all the trabeculæ of the sponge-work and the bridles are covered with an epithelium of flat epithelioid cells, which is continued also over the pia mater and the ligamentum denticulatum, and lines the tubular sheath-like prolongations of the space along the issuing nerve roots. The subarachnoid space therefore, like the subdural space, may be regarded as a serous or large lymphatic space, but it is an actual not a mere potential space; it always contains an appreciable quantity of fluid. The quantity present in the subarachnoid space of the cranial cavity is small, probably not exceeding 2 c.c. under normal circumstances; there is a larger quantity in the spinal canal. The fluid which escapes from these cavities when they are laid bare is called *cerebro-spinal* fluid; it is not ordinary lymph, but is furnished in a particular way, and deserves special study. To understand its nature and origin, we must turn to some special arrangements of the pia mater.

§ **694.** The pia mater proper, consisting of interwoven bundles of connective tissue, with some elastic fibres and a considerable number of connective tissue corpuscles, serves as we have said as the bearer of blood vessels to the nervous structures which it invests. The small arteries as they pass into the nervous substance by the way of the septa are surrounded by perivascular lymphatic canals with which spaces in the neuroglial groundwork both of the brain and spinal cord, especially spaces surrounding the larger nerve cells, are continuous. As is the case with other tissues, so with the central nervous system, the several elements of the tissue are bathed with lymph derived from the blood; and this, oozing through the spaces into the perivascular canals and the other lymphatic vessels of the pia mater, makes its way into the subarachnoid space; but the fluid in the subarachnoid space has other sources besides.

The roof of the fourth ventricle is, as we have said (§ 601), reduced to a single layer of non-nervous columnar epithelium, which appears as a mere lining to the pia mater overlying it. In the hinder part of the ventricle this roof is perforated by a distinct narrow oval orifice, the *foramen of Majendie.* By this orifice, which passes right through both the pia mater and the underlying layer of epithelium, the cavity of the fourth ventricle, and so the whole series of cavities derived from the original medullary canal, the lateral and third ventricles, the aqueduct, and the central canal of the spinal cord, are made continuous with the subarachnoid space. There are also two other less conspicuous communications between the subarachnoid space and the fourth ventricle, one on each side of the flocculus of the cerebellum. Hence the cerebro-spinal fluid is made common to all these cavities, and is furnished not only by the pia mater investing the outside of the brain and spinal cord, but also, and indeed probably to a larger extent, by the epithelium lining the several cavities of the cerebro-spinal axis, especially perhaps by those portions of that epithelium which coat the processes of pia mater projecting into those cavities at certain places.

We saw previously (§ 602) that a large fold of the pia mater, carrying in with it the thin non-nervous epithelium which alone represents at the place the original wall of the medullary canal, is thrust inward at the transverse fissure of the brain, beneath the fornix, to form the velum interpositum, thus supplying a roof to the third ventricle, and that it thence projects into each lateral ventricle as the choroid plexus of each side, reaching from the foramen of Monro in front along the edge of the fornix to the tip of the descending horn. The velum being a fold of the pia mater consists theoretically of two layers, and between the upper dorsal layer and the lower ventral layer, lies a thin bed of connective tissue carrying arteries forwards from the hind edge of the corpus callosum, and similarly carrying veins backwards; these vessels furnish the choroid plexus with an abundant supply of blood. In the choroid plexus, the folded pia mater is developed into a number of villus-like processes, the primary processes bearing secondary ones. Each process consists, like a villus, of a basis of connective tissue, in which the blood vessels end in close set capillary loops, covered with an epithelium. The epithelium, though continuous with the rest of the epithelium lining the lateral ventricle, and thus as we have said shutting off the lateral from the third ventricle (except at the foramen of Monro), and though like it derived from the wall of the original medullary canal, is different in structure. Over the ventricle generally the epithelium consists of ordinary short columnar, apparently ciliated, cells, with more or less transparent cell-substance; the cells over the choroid plexus are cubical, often irregular in form, and their cell-substance is loaded with granules, some of which are pigmentary. They have very much the appearance of 'active' secreting cells; and indeed a branched process of the plexus may be compared to an everted alveolus of a secreting gland, with the epithelium outside and the blood vessels within. It cannot be doubted that these cells play an important part in secreting into the cavity of the ventricle fluid which, passing thence by the foramen of Monro into the third and so into the fourth ventricle, finds its way by the foramen of Majendie into the subarachnoid space.

As the velum overhangs the third ventricle it sends down vertically two longitudinal linear fringes, which, resembling in structure the choroid plexuses of the lateral ventricle, are called the choroid plexuses of the third ventricle. From the roof of the fourth ventricle there hangs down on each side a similar linear fringe, the choroid plexus of the fourth ventricle, which is especially developed at its front end beneath the overhanging cerebellum. These subsidiary choroid processes doubtless assist in furnishing cerebro-spinal fluid, but their share is small compared with that of the main choroid plexuses of the lateral ventricle.

The fluid thus supplied by secretion in the ventricles mingles with the fluid supplied by transudation in the subarachnoid space. The subdural space though anatomically shut off from is physiologically continuous with the subarachnoid space, fluid passing readily from the one space to the other, and the fluid obtained from either of them may be considered as cerebro-spinal fluid.

§ **695**. *The Cerebro-spinal Fluid.* The specimens of cerebro-spinal fluid which have been examined as to their composition are not quite comparable with each other, since while some (such as those obtained from cases where a fracture of the base of the skull has placed the subarachnoid space at the base of the brain, where it is largely developed, in communication with the external meatus, and the fluid escapes by the ear) may be regarded as normal, others (such as those obtained from cases of hydrocephalus where the ventricles contain an unusual quantity of fluid, or from cases of spinal malformations) must be considered as abnormal.

In most of the more complete analyses, the fluid examined has belonged to the latter class; and the following statements apply, strictly speaking, to them alone.

With this caution we may say that cerebro-spinal fluid is a transparent, colourless or very slightly yellowish fluid, of faint alkaline reaction, free from histological elements. The specific gravity is about 1010 or less, the amount of solids being on an average 1 p.c. Of these by far the greater part, ·8 or ·9 p.c., is supplied by salts, the total quantity of which as well as the relative amount of the several constituents being about the same as obtain in blood and lymph. The comparative deficiency of solids is due to the scantiness of the proteids, which rarely exceed ·1 p.c. These are chiefly globulin and a form of albumose, or even peptone; albumin is said to be generally absent. The fluid, save apparently in exceptional cases, does not clot, and contains neither fibrogenous factors, nor fibrin ferment. It very frequently contains a substance which like dextrose reduces Fehling's solution but which is not a sugar; it appears to be pyrocatechin or a closely allied body.

Seeing that a fluid of such a composition is of a different nature from ordinary lymph, furnished entirely in the ordinary way, we might be inclined to infer that probably a very large part of the whole mass of the fluid is furnished by the secreting epithelium of the choroid plexus. But it must be borne in mind, that the foregoing analyses refer chiefly to fluid appearing under abnormal circumstances, and it would be hazardous to draw any wide inference from them. We have little or no exact experimental evidence as to how much fluid is actually secreted by the choroid plexuses; and if the fluids which have been analyzed do represent a mixture of ordinary lymph supplied through the pia mater with the peculiar secretion of the choroid plexuses, some further change beyond the mere mingling of the two fluids is needed to explain the remarkable absence of albumin which has been so strongly insisted upon by various authors. It is stated that when the cerebro-spinal fluid is quickly formed, as is the case when it is allowed to escape freely through an opening in the skull, the peculiarities spoken of disappear; the fluid then acquires the characters of an ordinary serous exudation.

§ **696**. We may fairly suppose that during life the fluid is continually being supplied, from the one source or the other; but we have no very exact knowledge as to the rate at which it is furnished. In the dog, the fluid has been observed to escape through an opening made into the subarachnoid space at a rate varying very largely under different circumstances, and ranging from 1 c.c. in 40 minutes to as much as 1 c.c., in 6 minutes, the total quantity discharged in 24 hours varying from 36 c.c. to 240 c.c. In the cases of fracture of the base of the skull mentioned above, a very considerable flow has been frequently observed. But in all such instances as the above the circumstances in one way or another are abnormal, and the flow observed in them cannot be taken as the measure of the normal supply. The rate of flow was found in the dog to be much increased by the injection of substances (normal saline solution) into the blood, but to be relatively little influenced by artificial heightening of arterial pressure. This has been put forward as indicating that the fluid is chiefly furnished as a secretion and not as an ordinary transudation of lymph; but it cannot be regarded as affording a valid argument.

The fluid being thus continually formed must always find a means of escape. This is probably supplied in part by the tubular prolongations of the subarachnoid space along the nerve roots; these are continuous with the lymphatic vessels of the nerves, and so with the lymphatics of the body generally; and in the skull, the passages of this kind along the cranial nerves, especially along the two optic nerves into the orbits, afford a ready means of escape. But there is evidence that in the brain much of the fluid escapes through the Pacchionian glands directly into the blood of the cerebral venous sinuses of the arrangements of which we shall presently have to speak. Indeed it has been urged that the chief absorption of cerebro-spinal fluid takes place not in the vertebral canal but in the cranial cavity and there chiefly by means of the Pacchionian glands. Fluid for instance disappears more readily when introduced into the cranial cavity over the bulb, than when introduced into the lower end of the vertebral canal.

The quantity of cerebro-spinal fluid present at any one time is the result of the balance then obtaining between formation and escape. Assuming the escape to be mainly by a process of absorption into the venous stream through the Pacchionian glands, there is evidence that this depends closely on the difference between the pressure of the fluid in the subdural (or subarachnoid) space and the pressure of the blood in the cerebral venous sinuses. If the venous pressure be lowered or the pressure of the fluid be raised absorption is increased, until by the process the two pressures are again made equal. If this be so, since the venous pressure is subject to variations, the pressure of the cerebro-spinal fluid must also be subject to variations, but to variations which are temporary only, since the latter is always striving to accommodate itself to the former. Hence any such statement as that in the dog the average pressure of the fluid in the subarachnoid space is about 10 mm. of mercury has relatively little value; indeed the brain is said to work well within a range of this pressure from zero to 50 mm.

Variations then in the quantity and in the pressure of the cerebro-spinal fluid may be traced to variations in absorption dependent on venous pressure. Whether variations of the fluid due to variations of formation are similarly due to variations in venous pressure is not so clear; nor indeed do we at present fully understand what circumstances definitely determine these.

The rate of possible escape is not without importance as regards the mechanical importance of the cerebro-spinal fluid. Thus it has been urged that when an extra quantity of blood is driven into the skull, any injurious intercranial compression is prevented, not only by the transference of a quantity of cerebro-spinal fluid through the foramen of Majendie from the cranium into the spinal canal, the walls of which are less rigidly complete, but also by the direct escape of the fluid from the cavity of the skull in the manner described. It has also been urged that the fluid at the base of the skull, in the large subarachnoid spaces of which it gathers in larger quantity than elsewhere, acts as a sort of protective water cushion to the delicate cerebral substance, and that, in general, the presence of the fluid is mechanically useful to the welfare of the brain, removal of the fluid by aspiration being said to lead to hæmorrhage from the pia mater and to various nervous disorders. But this view exaggerates the quantity of fluid present in the cranium, which as we have said is probably small; and indeed our knowledge as to the part which the fluid plays is at present very imperfect; its peculiar chemical characters suggest that it has some chemical as well as mechanical functions.

SEC. 13. THE VASCULAR ARRANGEMENTS OF THE BRAIN AND SPINAL CORD.

§ 697. The blood vessels reach the nervous structures by means of the pia mater. In the spinal cord arteries coming from the vertebral, intercostal and other arteries, and travelling along the nerve roots join the pia mater, and then through the fissures and septa reach all parts of the cord; but as we have previously remarked the capillary network is much denser, and therefore the blood supply much greater in the grey than in the white matter. The veins, also gathered up along the septa and fissures into the pia mater, those coming from the grey matter forming, before they reach the external pia mater, a conspicuous longitudinal vein on each side of the posterior grey commissure, pass from the pia mater to the large venous sinuses of the dura mater and so to adjoining veins.

In the brain two important features of the distribution of the arteries deserve special attention. In the first place, the quadruple supply by the right and left vertebral and internal carotid arteries is made one by remarkable anastomoses forming the *circle of Willis.* The right and left vertebral arteries entering the vertebral canal at the level of the 6th cervical vertebra, and running forwards towards the brain, join beneath the ventral surface of the bulb to form the single median basilar artery. This, after giving off branches to the bulb, cerebellum, and pons divides into the right and left posterior cerebral arteries. Each internal carotid entering the skull reaches the base of the brain in the region of the floor of the third ventricle, and, passing ventral to and athwart the optic tract, gives off the large and important middle cerebral artery along the fissure of Sylvius, and then, turning forwards and towards the median line, passes dorsal to the optic nerve to end in the anterior cerebral artery. Just however as it gives off the middle artery, it sends backwards, inclining to the middle line, a relatively large branch, the posterior communicating artery, which joins the posterior cerebral near the origin of this from the basilar artery. Moreover, the two anterior cerebral arteries soon after they have crossed the optic nerves, just as they are about to run straight forwards along the frontal lobes, are joined together by a short wide branch, the anterior communicating artery. In this way the vertebral arteries through the basilar artery join with the carotid arteries to form around the optic chiasma beneath the floor of the third ventricle an arterial circle, the circle of Willis.

Blood can pass along this circle in various ways; from the basilar artery along the right posterior communicating artery to the right internal carotid, and so by the right anterior cerebral artery and anterior communicating artery to the left side of the circle, and similarly from the basilar artery along the left side to the right, or from the right or from the left carotid through the circle, to the right hand or to the left hand in each case. Since the channel of the circle is a fairly wide one, the passage in various directions is an easy one; all the vessels radiating from the circle, including the basilar artery and its branches, can be supplied by the carotids alone, or by the vertebrals alone, or even by one carotid or one vertebral alone. In this way an ample supply of blood to the brain is secured in the face of any hindrance to the flow of blood along any one of the four channels.

In what may perhaps be considered the usual arrangement, the calibre of the posterior communicating arteries is rather smaller than the other parts of the circle, so that, other things being equal, most of the vertebral blood will pass by the posterior cerebral arteries, while the carotid blood passes to the middle and anterior cerebral arteries; but many variations are met with. We may also here perhaps call to mind the fact that the left carotid coming off from the top of the aorta, offers a more straight path for the blood than does the right carotid which comes off from the innominate artery.

Another special feature of the arterial supply to the brain is that the three large cerebral arteries, posterior, middle and anterior, are distributed almost exclusively to the cortex and to the subjacent white matter, while the deeper parts of the hemisphere, the nucleus caudatus, thalamus and the like, with the internal capsule and other adjoining white matter are supplied by smaller arteries coming direct from the circle of Willis, or from the very beginnings of the three cerebral arteries. It is stated that these two systems make no anastomoses with each other; but this appears to vary much in different individuals. The region of junction between the two systems seems to be more liable than do other parts of the brain to suffer in its blood supply when general difficulties arise in the circulation; this perhaps explains why central 'softening' due to imperfect nutrition is especially frequent in that important cerebral structure, the internal capsule. We may add that the anterior cerebral artery supplies the cortex of the dorsal aspect of the frontal lobe as well as the front and middle portions of the whole mesial surface of the hemisphere; that the middle cerebral, always large, is distributed to the side of the brain, that is, the parietal lobe, with the ventral part of the frontal lobe and the dorsal part of the temporal lobe; and that the posterior cerebral supplies the rest of the cortex, that is to say, the occipital lobe including the hind part of the mesial surface of hemisphere, together with the ventral part of the temporal lobe. The distribution of these arteries therefore does not correspond to functional divisions, for while the middle cerebral supplies a large part of the Rolandic region, it does not supply the whole of it, and does supply parts outside it. Though the small arteries as they run in the pia mater on the surface of the cortex anastomose freely, there is very little anastomosis between the small arteries which leaving the pia mater dip down into the substance of the brain; hence when these latter arteries are blocked, the nutrition of the part of the cortex supplied by them is apt to be impaired.

§ **698.** The venous arrangements of the brain have very special characters.

Along the upper convex border of the sickle-shaped fold of dura mater, the falx cerebri, is developed a large venous sinus, the *superior longitudinal sinus.* This, triangular in section, increasing in calibre, from before backwards, is a sinus, not a vein; its walls are formed of nothing but connective tissue lined with epithelium, muscular elements being entirely absent. Though its channel is broken by bridles of connective tissue passing across it, it possesses no valves, and indeed these are absent from all the sinuses and veins of the brain. Most of the blood returning from the cortex and subjacent white matter is carried into this sinus by veins, the mouths of which are for the most part directed forwards, that is to say, against the direction of the blood stream. Along the lower concave border of the falx is a similar sinus, the *inferior longitudinal sinus*, which however is small and into which relatively few veins open.

From the deeper parts of the brain, and especially from the choroid plexus, blood is conveyed by the *veins of Galen* along the velum interpositum to the transverse fissure, where the veins of Galen join the inferior longitudinal sinus to form the *straight sinus.* This, running along the line formed by the intersection of the vertical falx with the (more or less) horizontal tentorium, joins the end of the superior longitudinal sinus to form the reservoir or cellar, called the *torcular Herophili*, from which the *lateral sinus*, passing on each side along the convex border of the tentorium and gathering veins from the cerebellum and hind regions, as well as from the base of the brain, delivers the blood into the internal jugular vein.

It should be added that veins from the nose and, through the ophthalmic veins, from the face join the veins and sinuses of the brain, and that the so-called emissory veins pass through the cranium from the scalp to the superior longitudinal and lateral sinuses.

The channels for the venous blood of the brain are therefore not veins but sinuses, which while affording an easy onward path can also be easily filled and easily emptied, and in which the blood can move to and fro without the restrictions of valves. This arrangement is correlated to the peculiar surroundings of the brain, which is not like other organs protected merely by skin or other extensible and elastic tissue, but is encased by a fairly complete inextensible envelope, the skull. As a consequence of this, when at any time an extra quantity of blood is sent from the heart to the brain, room must be made for it by the increased exit of the fluids already present. When general arterial pressure is raised, more blood, as we shall see later on, is sent to the brain; the arteries, capillaries and small veins are expanded and filled with blood; and the whole volume of the brain is increased. The brain substance is incompressible, and hence extra room must be found within the rigid skull for the increased volume of the brain. This is in part provided for by the escape of cerebro-spinal fluid either into the vertebral canal, or out of the subarachnoid and subdural spaces into the venous blood stream or elsewhere. But, as we have seen, the quantity of fluid in the cranial subarachnoid and subdural spaces is small, as indeed is also that within the ventricles; hence the extra space thus provided is small. Further space is afforded by the escape of venous blood from the sinuses owing to their compression by the expanding brain; but this also is limited. The compression goes on only so long as the pressure of the brain-substance, that is the pressure in its blood-vessels, is greater than the venous pressure in the sinuses. But the latter is continually being raised by the former, until, at last, the difference ceases. The whole energy of the arterial pressure, which previously was partly spent in expanding the brain and pressing on the cerebro-spinal fluid and venous sinuses, is now entirely spent in driving the blood onward. Hence the main effect of a rise of arterial pressure is to increase the rapidity of the cerebral blood-stream. This is the effect provided that the general venous pressure, that for instance in the right auricle, remains normally low. In a normal circulation increase of arterial pressure, what is sometimes called arterial congestion, does not and indeed cannot lead to 'compression' of the brain, that is to compression of the brain-substance; its one effect is to quicken the blood-flow. The case is different if the venous outflow be obstructed as in so-called venous congestion; then compression of the brain substance may take place causing loss of consciousness and interfering otherwise with the brain's work.

§ **699.** The supply of blood to the brain seems at first sight not to correspond to the importance of this the chief organ of the body. In the rabbit it would appear that hardly more than one per cent. of the total quantity of the blood of the body is present at any one time in the brain, a quantity but little more than half that which is found in the kidneys; and while the weight of blood in the brain at any one time amounts to about five per cent. of the total weight of the organ, being about the same as in the muscles, in the kidney it amounts to nearly twelve per cent., and in the liver to as much as nearly thirty per cent. Making every allowance for the relative small size and small functional importance of the rabbit's brain, we may conclude that the blood-supply of even the human brain is likewise small; and making every allowance for rapidity of current, the interchange between the blood and the nervous elements must also be small. When we compare in an animal, in a dog for example, the change as to its gases which the blood undergoes in its passage through the brain with that which it undergoes in passing through a muscle, we find that the consumption of oxygen and production of carbonic acid is very much less in the former than in the latter, when both are in a condition which may be considered that of rest. When the muscle enters into a state of contraction this metabolism of rest is as we know very largely increased; but when the brain is excited, as in an epileptic fit, no marked increase of its metabolism can with certainty be noted. In other words, the metabolism of the brain-substance is of importance not so much on account of its quantity as of its special qualities.

The circulation in the brain may be studied by help of various methods. A manometer may be connected with the peripheral end of the divided internal carotid artery, a second manometer being attached in the usual way to the central portion. Since the peripheral manometer records the blood-pressure in the circle of Willis transmitted along the peripheral portion of the carotid artery, variations of pressure in the circle of Willis may thus be studied; and a comparison of the peripheral with the central manometer will indicate what general changes are taking place in the circulation through the brain. Thus a fall of pressure in the peripheral manometer unaccompanied by any corresponding fall in the central manometer would shew that the "peripheral resistance" in the brain was being lowered, in other words, that the vessels were being dilated.

In another method, in the dog, the outflow of venous blood from the lateral sinus through the posterior facial vein has been measured. The freedom with which blood passes along the sinuses justifies the assumption that the outflow through the open vein gives an approximate measure of the rate of flow under natural conditions; still the results are only approximate, and besides, the continued loss of blood introduces error.

A third method is a plethysmographic one. The skull is made to serve as the box of the plethysmograph or oncometer (§ 410); a small piece of the roof having been removed by the trephine, a membrane is fitted to the hole, and the movements of the membrane are recorded by help of a piston and lever or directly by a lever. In young subjects, the fontanelle, or portion of the cranium not yet ossified, may be utilized as a natural membrane, and its movements recorded in a similar manner. When the instrument is fitted to the hole in a water-tight manner, this method records variations in internal pressure; and we may take it for granted, unless otherwise indicated, that greater or less pressure is due to more or less blood passing to the brain. But the amount of pressure brought to bear on the recording instrument will also depend on the readiness with which the cerebro-spinal fluid escapes from the cavity of the skull; if there be a hindrance to the escape, or on the other hand an increased facility of escape, the same increase of supply of blood will produce in one case a less, in the other a greater movement of the lever. If the membrane be attached loosely to the hole so as to allow free escape of the cerebro-spinal fluid, the lever practically resting on the surface of the cerebral hemisphere, the method records variations in the dorso-ventral diameter of the hemisphere, and these may be taken as measuring variations in the volume of the brain and so in the blood supply. In neither form, however, does the method by itself give us all the information which we want. An increase of blood in the brain, and therefore an expansion of the brain, and so a movement of the recording instrument, may result either from a fuller arterial supply or from hindrance to the venous outflow; the former condition is, at least in most cases, favourable to, the latter always and distinctly injurious to, the activity of the nervous structures; hence the teachings of the lever must be corrected by a simultaneous observation of the general arterial pressure and of the blood-pressure in the veins of the neck. Moreover, the argument which we used (§ 417) in reference to the kidney may be applied here and probably with equal force, namely, that the value of the blood stream for the nutrition of the tissue is dependent not alone on the amount of blood-pressure, but also and especially on the rapidity of the flow; indeed this second factor is of particular importance in view of the need of supplying the nervous elements with an adequate interchange of gases. Now of the rapidity of flow the plethysmographic method can give us indirect information only.

A fourth method which has been more recently introduced gives perhaps the most trustworthy results of all. This consists in simultaneously recording (1) the arterial pressure in a carotid artery, (2) the venous pressure in the right auricle, (3) the venous pressure in a cerebral sinus, and (4) the pressure in the subdural space; for the latter three measurements a manometer filled with saline fluid is used.

§ **700.** By one or other or all of these methods, but especially by the last, certain important facts have been made out. The volume of the brain, as determined by the amount of blood present in it, is continually undergoing changes brought about by various causes. Each heart-beat makes itself visible on the cerebral as on the renal plethysmographic tracing, and as we have seen in speaking of respiration, the diminution of pressure in the great veins of the neck during inspiration leads to a shrinking, and the reverse change during expiration to a swelling of the brain. The plethysmograph also shews variations, larger and slower than the respiratory undulations, and brought about by various causes, such as the position of the head in relation to the trunk, movements of the limbs, modifications of the respiratory movements, and apparently phases of activity of the brain itself, as in waking and sleeping; undulations corresponding to the Traube-Hering variations (§ 387) of blood-pressure may not unfrequently be observed.

All the various methods shew that the flow through the brain is largely determined by a vaso-motor action of some kind or another. And this we might indeed infer from ordinary experience. When the head is suddenly shifted from the erect to a hanging position, there must be a tendency for the blood to accumulate in the cranial cavity, and conversely when the head is suddenly shifted from a hanging to an erect position, there must be a tendency for the supply of blood within the cranium to be for a while less than normal. Either change of position, and especially perhaps the latter, would lead to cerebral disturbances, which in turn would in ourselves be revealed by affections of our consciousness. Indeed the effects of rapidly changing the position of the body afford a most delicate test of the efficiency of the vaso-motor mechanism. That a perfectly healthy, and especially young organism whose vaso-motor mechanisms are at once effective and delicately responsive, can pass swiftly from one position of the head to the other without inconvenience, whereas those in whom the vaso-motor mechanisms have by age or otherwise become imperfect are giddy when they attempt such rapid changes, is in itself adequate evidence of the importance of the vaso-motor arrangements affecting the circulation through the brain. The several methods agree in shewing that increased general arterial pressure, such as that for instance induced by stimulation of a sensory nerve, leads to a greater flow of blood to or rather through the brain; the volume of the brain is somewhat increased and the venous outflow is greatly quickened. Conversely, a lowering of arterial pressure leads to a lessened flow of blood to or through the brain. Owing to the surroundings of the brain, the mere quantity of blood present in it does not vary widely; that remains fairly constant; but the vaso-motor influences do largely influence the rate of flow, which in respect to the metabolism of the brain is of high importance.

Seeing that the cerebral arteries have well-developed muscular coats, the basilar artery in fact being conspicuous in this respect, one would be led to suppose that the brain possessed special vaso-motor nerves of its own; and recognizing the importance of blood supply to rapid functional activity one would perhaps anticipate that by special vaso-motor action, the supply of blood to this or that particular part of the brain might be regulated apart from changes in the general supply. Though nerve-fibres have recently been described as distributed to the cerebral vessels, the various observations which have hitherto been made have failed to demonstrate with certainty any such special vaso-motor mechanisms directly governing cerebral vessels. It would be hazardous to insist too much on this negative result, especially since the observations have been chiefly directed to the nerves of the neck, the experimental difficulties of investigating the presence of vaso-motor fibres in the cranial nerves being very great. Still it may be urged and indeed has been urged that the flow of blood through the brain is so delicately responsive to the working of the general vaso-motor mechanism just because it has no vaso-motor nerves of its own. In such an organ as the kidney, an increase of general blood-pressure, as we have more than once insisted, may or may not lead to a greater flow through the kidney according as the vessels of the kidney itself, through the action of the renal vaso-motor nerves, are dilated or constricted; and, as we have seen, a constriction of the renal vessels may be one of the contributors to the increased general pressure. In the brain, on the other hand, an increase of general arterial pressure seems always to lead to increase of flow. Thus in the Traube-Hering undulations just mentioned, the expansions of the brain are coincident with the rises of the general pressure, whereas in the normal kidney and in other organs the local Traube-Hering undulation reverses the general one, the shrinkings are synchronous with the rises of pressure, the local constriction being one of the factors of the general rise. It is argued, that in the absence of vaso-motor nerves of their own, the cerebral vessels are wholly, so to speak, in the hands of the general vaso-motor system, so that when the blood-pressure is high owing to a large vaso-constriction in the abdominal viscera, more blood must necessarily pass to the brain, and when again the blood-pressure falls through the opening of the splanchnic flood-gates (§ 173) less blood necessarily flows along the cerebral vessels. On this view the vaso-motor mechanism by which, as mentioned above, we accommodate for changes in position is not cerebral but abdominal. The tendency of the erect position to drive the blood by hydrostatic pressure from the brain into the abdomen is under normal conditions compensated for by the tonic vaso-constriction of the splanchnic blood vessels. In the recumbent position this constrictive grasp is slackened, otherwise too much blood would pass to the brain. In passing rapidly from the recumbent to the erect position, or *vice versa*, the vaso-motor splanchnic mechanism in a healthy organism responds, with a tightened or with a slackened grasp, rapid enough to secure that no great change in the blood supply to the brain takes place in either case. When the vaso-motor mechanism is impaired as by old age or temporarily weakened in its action by anæsthetics the compensation may be insufficient. Hence in profound anæsthesia it is dangerous to raise the subject suddenly from the recumbent to the erect position; the splanchnic compensatory constriction may be inadequate and the brain rendered anaemic. So, when fainting, as is often the case, is the result of diminished splanchnic constriction, too much blood is being collected in the abdomen and too little sent to the brain, the condition is at once checked by a change from the erect to the recumbent position. It would seem that this vaso-motor compensating mechanism is better developed in man and the monkey with erect posture than in the lower animals; these latter are apt to compensate not enough or too little.

In this relation of the splanchnic vaso-motor mechanism to the brain we may recognize a sort of self-regulating action. The effects of acute cerebral anaemia, of rapidly withholding blood from the brain are, put briefly, loss of consciousness, with respiratory spasms followed by a rise of blood-pressure and a slowing of the heart-beats, which condition, if the anaemia continue, gives way to a fall of blood-pressure with a rapid pulse and so brings about death. That is to say, the spinal bulb sharing in the anaemia, the bulbar vaso-motor centre is by the lack of blood first stimulated and then exhausted, the cardio-inhibitory centre sharing the same fate. Hence diminished supply of blood to the brain, by exciting the bulbar vaso-motor centre, leads to increased constriction in the splanchnic area and so tends to drive more blood to the brain; thus the injurious effects to the brain threatened by an anaemic condition are warded off by the very beginning of the anaemia itself.

§ **701**. All the above advantages are, however, quite compatible with the coexistence of special vaso-motor mechanisms. Moreover it is obvious that such a general action of the vaso-motor mechanism as we have just expounded can only affect the brain as a whole. But, as we have seen, the whole tendency of modern investigation has been to emphasize the localisation of function as regards the cortex. Hence there seems to be a contradiction between the one line of inquiry and the other. Possibly what we have just described is only the coarser and more obvious part of a mechanism the finer and more delicate adjustments of which have yet to be learnt. Indeed the flow of blood through the brain, as measured by the venous outflow, may be modified independently of changes in the general blood-pressure. For instance, stimulation of the Rolandic region of the cortex quickens the venous outflow, without producing any marked change in the general blood-pressure; this feature becomes very striking at the onset of epileptiform convulsions when these make their appearance. It is difficult not to connect such a result of functional activity with some special vaso-motor nervous arrangement comparable to that so obvious in the case of a secreting gland. Again, it has been observed that certain drugs have an effect on the volume of the brain, quite incommensurate with their effect on the vaso-motor system; thus in particular the injection into the general blood stream of a weak acid produces a large and immediate expansion of the brain, while the introduction of a weak alkali similarly gives rise to similar considerable shrinking. It is suggested that these effects are produced by the acid or alkali acting directly on the muscular coats of the minute arteries and so leading to relaxation or contraction respectively. In treating of the chemistry of nervous substance (§ 72) we stated that the grey matter of the cortex is faintly alkaline during life and under normal conditions, but becomes acid after death or when its blood-supply is interfered with; and it has been urged that nervous grey matter like muscular substance developes acidity during activity, as well as upon death, the acidity being probably due in each case to some form of lactic acid. And just as it has been suggested that the dilation of the minute arteries of a skeletal muscle, accompanying or following the contraction of the muscle, is brought about by the acid generated during the contraction causing a relaxation of the muscular coats of the minute arteries, so it has been suggested that a similar acidity, the product of nervous activity, similarly leads in nervous tissue to a dilation of the vessels of the part. It has indeed been urged that in the above observations sufficient heed was not paid to variations in the venous pressure. But the phenomena probably cannot be wholly thus explained; and of them and others the existence of special vaso-motor mechanisms would afford a more satisfactory explanation than that given; in spite of the negative results so far obtained, the matter is obviously one needing further investigation. Meanwhile we have abundant evidence that, however brought about, the flow of blood through the brain, and probably through particular parts of the brain, is varied in accordance with the needs of the brain itself and the events taking place elsewhere in the body.

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